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THE VIRGINIA JOURNAL OF SCIENCE

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The Role Of Statistics In Scientific Research

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There is a good deal of misunderstanding about the scope of statistics even, perhaps, among the scientists who are accustomed to using statistical methods. I would like to give a broad account of the basic nature of the subject and to explain also why statisticians are such peculiar beings and manage to find some kind of interest even in what many think to be the most uninteresting of all subjects.

THE NATURE OF THE STATISTICAL METHOD

I begin by dismissing certain misconceptions about statisticians. There is a story that at the outbreak of war the Army, wanting some advice in the engagement of its professional personnel, sent a letter to one of the universities, saying: "The Army requires the following expert personnel: two cooks, three butchers, two statisticians." That is the level on which many people place the occupation of a statistician, as a numerical hack who adds up a column of figures.

Now, it is true that the statistician is concerned with numerical data, and it is easy to draw the inference that his primary interest lies in the actual handling of such data; but that is to misunderstand the essentials of the statistical approach. One might as well say, for example, that an artist is primarily interested in the properties of paint or that the astronomer is primarily interested in measuring the right ascension of stars. The statistician uses numerical material but he is always trying to find some truth about the physical world that lies behind them. Numbers are the raw material of his craft, and have a certain fascination of their own, but they are not in themselves the ultimate object of his research.

The statistician, in fact, is concerned with the properties of aggregates, and statistics, as far as definition is possible, may be defined briefly as that branch of scientific method which deals with assemblies, collections, or aggregates. In one sense, practically the whole of science, in the sense of organized knowledge about the external world, is concernd with collections of one kind or another, even if only with collections of observations of a particular situation. Statistics is man's attempt — the most successful attempt, I think, up to date — to cope with the complexity of things and to reduce them to law and order. It used to be said that mathematics was the matrix of the sciences. Nowadays it is statistics which is the matrix of the scientific method, moulding in some way practically the whole field of scientific endeavor. That may seem rather a large claim

to make, and I make it in all humility; but that is, in fact, the thesis that is to be developed. I shall begin by showing in some detail how particular statistical ideas or particular branches of statistical methods are applicable in an enormous number of different sciences.

Some groups of problems: (*a*) *Gambler's ruin.*—I shall consider three groups; the first of them arises in a very old form as the problem of the ultimate ruin of the gambler. In its simplest form, we consider two players, A and B, who are playing a fair game such as one might get if he were tossing an unbiased coin and betting on whether it fell heads or tails. This situation leads to all sorts of topics in probability, one of the most important being the proposition to the effect that if A has a much larger stake than B, it is very nearly certain that A will ruin B; and that one can see without any detailed mathematics, because there will occur long and short runs of bad luck, and the man with the smaller stake is the man who is least able to withstand them. Consequently, if he is unable to borrow, there will almost surely come a time when he is ruined. In particular, the inference which is usually drawn from this is that if one man is gambling against a set of people with practically infinite resources, the result is that he is morally certain to be ruined. This is the famous theorem of the ultimate ruin of the gambler; for he plays against the rest of the world and hence against practically unlimited resources.

I am not concerned, however, nor is the statistician concerned, with the moral implications of such results. You might suppose that apart from such implications, theorems of this type have no very direct application outside the field of gambling itself; but it is there that the statistical viewpoint begins to assert itself, for in a sense, a great many of the decisions that we make, in science as well as in ordinary life, are in the nature of gambling. For example, in sampling (and a very great deal of scientific thought is based on samples of some kind or another), we are rarely able to make a categorical assertion about the population; we take a gamble on the truth of certain inferences drawn from the sample. We express our conclusions in terms of probability. We are never sure; we make as sure as we can, that is to say, we try to cut down the risk to a minimum; but we can rarely eliminate it altogether.

This basic idea has led to a very large number of applications. For example, during the war, when sampling was carried out very extensively in the testing of certain components which were being manufactured on a very large scale, there occurred the problem of economy in the sample size. The extreme case, perhaps, is the one in which we have what is called destructive sampling. If we are manufacturing bullets or shells, there is only one really satisfactory way of finding out whether the bullet is a good one, and that is by firing it. But we cannot test all our bullets in such a fashion and still have a supply to use on the enemy, so we have to take samples; and in order to get the testing process performed as quickly as possible, we try to economize in the amount of sampling that we do.

Consider a two-dimensional network of the kind shown in Figure 1. We choose our objects for test one by one, and to any sequence of objects

we associate a path on the network in the following simple way: beginning at the origin we move one step to the right if the first object is a 'success", *i.e.* passes our test, and one step in the vertical direction if it is a failure, *i.e.* does not pass the test; similarly for the second object, beginning at the end of the path corresponding to the first object; and so on. A random set of objects will then correspond to a random walk on this network. Now if we decide, on prior grounds, that we are prepared to tolerate a fraction x per cent failures in the total population from which our sample is drawn, and that we wish to make a correct judgment in y per cent of the cases whether this fraction is exceeded or not, we can set up, by calculations based on the theory of probability, certain barriers such as A and B on the network and proceed as follows: we trace the path corresponding to the observed sample until it strikes one of the barriers. If it strikes A we accept the population as having not more than x per cent failures; if it strikes B we reject the population. This is a simple case of what is known as sequential sampling.

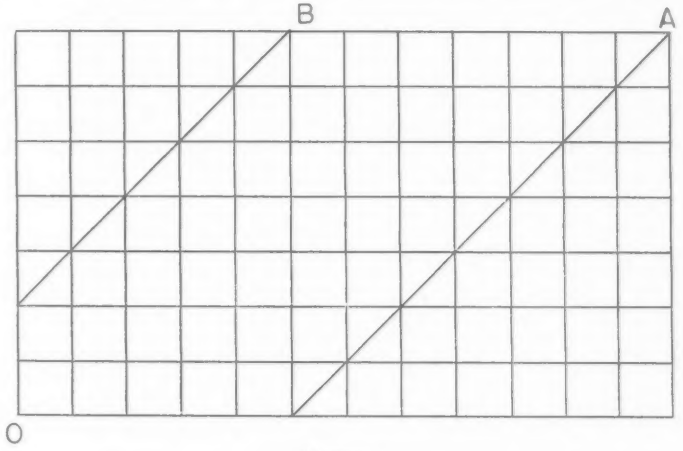

Figure 1.

Now this is very much the situation which we study in the problem of the ruin of the gambler. In the simple version we are considering bound A corresponds to a man with a certain amount of stake represented by a. B corresponds to a second player with stake b. If we reach bound A the first player is ruined (we accept the population), if we reach B the second player is ruined (we reject the population). Whether we accept or reject in a number of trials thus corresponds to the relative frequencies with which gamblers like A and B will be ruined in games of this type. By using propositions derived from the theory of such games we managed, by the development of sequential sampling, to cut down the

average sampling required on destructive sampling by about fifty per cent.

To take another illustration – and I am jumping from field to field as sharply as I can – I refer to a genetical problem which in its simplest form can be stated as the proposition that ultimately everybody's surname will be Smith. Let us put the case in its simplest form: suppose that every married couple has only two children, so that the population reproduces itself, and that all children intermarry. Let us also suppose that the probability of any child being male is ½. Then a male child perpetuates the surname but a female child loses it. Thus the chance of perpetuation is ½ and over a number of generations the chance of survival is very much what it would be if that surname were gambling against all the others in a fair game with an even chance of winning at any one throw. Now by historical accident the Smiths have got themselves into an advantageous position, that is to say, they have a large stake, and it is therefore virtually certain, in the sense of the theory of probability, that the other surnames cannot compete. There will be a run of bad luck which will extinguish them, and so in the course of time, everybody's surname will be Smith, in the same way that in gambling all the money ultimately is concentrated in one hand. You may not think perhaps that this particular effect is very important, but if you replace surnames by certain genetic characteristics the question of survival obviously can become of extreme importance. The actual situation governing the transmission of biological characteristics is, of course, much more complex, but fundamentally, under random mating, is the same as in the problem of the gambler.

I take a further generalization of the gambling situation. The case we have already considered may be regarded as a random walk on a network under two conditions: one is that one has a choice of only two directions (horizontal or vertical) and the other is that one always moves outwards from the origin and never return towards it. If we remove those restrictions, we get a more general random walk problem.

Let us suppose that a mosquito starting from a malarial site at 0 in Figure 2 flies the same distance each day – I am over-simplifying the situation, of course – but chooses its direction at random. The mosquito might perform the kind of path shown in the diagram and at the end of n days it will be a certain distance from its origin. Again we have, in a sense, a gambling problem. We are interested in the question how far that mosquito has proceeded from his center after a certain period of time; but this is not a determinate distance; it depends on the chances inherent in the random choice of directions. It is a problem in pestology where we want to know, for example, how rapidly we shall get a spread from the infected place. Clearly, under random conditions there will be very few cases in which the mosquitoes will fly in the same direction on successive days, so there will be a rather thin scattering on the boundary, but there will be quite a lot of them in which the mosquitoes return more or less to the neighborhood of the starting point, so that we get a sort of heaping up of the density around the original site of infection, and

the plague will spread outward; and it is in the rate of spread of similar vector borne diseases that the immunologist is interested.

To go from mosquitoes to the theory of sound; there is a similar problem in which we have an incoming train of sound waves, and we are concerned to know whether they are really 'noise" (in the sense of being composed of elements with random phase) or whether there are systematic harmonic components present. We can represent the situation as a kind of mosquito flight, in which the amplitude of any component corresponds to the length of the flight and the phase to the direction. If the signal we receive is noise, these phase angles are more or less at random. Thus we can examine the presence of systematic components by using, in a different context, the theory of the random walk.

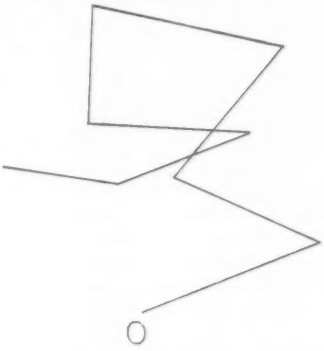

Figure 2.

Finally, to go from pure physics to economics, we require the same kind of theory in the analysis of the trade cycle. Suppose we have a time series which is thought to incorporate certain systematic oscillatory properties. We analyze the series into harmonic constituents, and our interest is in testing whether the effects which emerge are significant. This again brings us to the problem of ascertaining whether a "random walk" of harmonic components presents evidence of systematization or not.

Thus, starting out from what appears to be a highly formalized problem in gambling, we find applications to industrial standardization, genetics, immunology, physics, and economics. A large number of different physical situations present to the statistician, on analysis, a unified class of problems in random variation. Thus, the way in which the statistician branches out into other fields and has fingers in all sorts of pies becomes obvious.

Some groups of problems: (*b*) *the theory of queues.* —I take another group of examples of this kind. We have, in England, what we call a queue (the American equivalent, I think, is a line-up) in which a number of individuals wait in a line for some sort of service; for example, human beings waiting for a bus, or automobiles waiting for attention at a service station. We set up a conceptual situation in which we have a number

of individuals lined up for some kind of attention. We suppose that their input has a certain pattern, the queue is subject to certain rules, and the service-time has a certain output or pattern. We are interested in the behavior of the queue under certain hypotheses concerning these patterns, *e.g.*, what is the most efficient ratio of service-time to the average input time, whether the queue is going to get out of hand in the sense that it grows too long, or whether there is a waste of time in the sense that so many resources are diverted to the output service that some of them are idle for substantial periods of time, and so on. Now that again may appear to you a highly abstract situation with few fields of application. In fact, it conceptualizes a class of problems with very wide and important applications. Historically, I believe, it first arose for study in problems connected with the control of telephone traffic and the design of a telephone switchboard. Consider, for example, a number of incoming calls on a switchboard; in general, there will be a queue of them on the lines; there will be a service mechanism represented either by an actual human operator or by a mechanical device. Given the number of subscribers and the pattern of incoming calls we may require to know how big our switchboard must be, how many people we want to employ on it, what is the most economic setup, *etc.*

What applies to telephone traffic is obviously extensible at once to other sorts of traffic. Consider, for example, the design of road traffic signals. Here, instead of having a single queue, we have a double queue of traffic moving in opposite directions, or in more complicated places such as crossroads and circuses we may have more. A typical problem now is to know how often street lights must change in relation to the known intensities of traffic, in order to achieve a minimum waiting time on the average, but also with certain further conditions; for example, we must also try to avoid such a long queue as to block previously occurring cross-streams of traffic. A similar type of problem arises in the design of aerodromes, where we have a limited air strip, and a large number of aircraft taking off or coming in. This is the kind of problem that was a very serious one during the war when we had a large number of bombers coming back from a raid, some of them badly shot up and therefore requiring special attention, and all of them queueing up in the air waiting for the service of landing. Again, we have a situation involving an influx of random arrival and an output of, not necessarily random but not always systematic, discharge in the form of the servicing mechanism.

A situation of a somewhat different kind occurs in industrial engineering. Suppose we have a number of looms which are spinning cotton. Every now and then a thread breaks and the corresponding machine automatically stops. We therefore have certain service operators present to mend these threads when they break. If we have only one operator looking after a number of machines, there may be a queue of machines waiting for service, and we may lose a great deal of machine time. On the other hand, if we have one operator to each machine, he spends ninety-nine percent of his time in reading a newspaper. Between these two extremes, there is an optimum situation, in which we get the best of both

worlds by economizing in the machine-time and balance the loss of time against the cost of the labor service. Here again, we have a rather more complicated queueing system in which we have, in general, a multiple input and possibly also a multiple output. You can see, without my elaborating the point, that the same idea may run all the way through an enormous number of applications wherever we have servicing mechanisms and a number of individuals coming in to make use of them.

Some groups of problems: (*c*) *the theory of preferences.*—I would like to take one further group of cases by way of exemplification, in a rather different field, namely, in the theory of preference. Here we are interested purely in the situation which arises when a certain number of people consider a certain number of objects and express preferences between them, as for instances when a number of consumers express preference between varieties of ice cream. The applications of this situation are again numerous and varied. For example, the whole system of academic examinations is effectively based on preference; the examiner has by some means or other to arrange his subjects in a rank order, and a rank order is a particular case of a set of preferences. An industrial example arises from spraying paint on a motor car where we have a number of different kinds of lacquer being applied, a number of different individuals doing it, a number of different methods of doing it, and finally, we have no objective means of measuring the excellence of the lacquer on a car. All we can do is to get a number of judges to express preferences, and so, out of the resulting scheme of preferences expressed by judges who themselves may be fallible, we have to try to allocate sources of differences between the types of paints, the types of methods, the types of operators, and the types of judges.

We use a similar technique based on preferences in studies of social mobility – I choose this example from the field of sociology because it is one of the most recent ones; for example, suppose we are interested in finding out whether people can move from one social class to another more easily now than they could fifty years ago, which is quite an important social problem from some points of view. We go to a number of individuals and ask them what their occupation is and what their father's occupation was; and we also ask their fathers, if we can locate them – or the individual if we cannot – what was the grandfather's occupation. We then have a sort of situation in which, if you classify these occupations into certain grades, any man who is now, say, in grade 3 may come from the higher grades 1 or 2, or from grade 3, or from lower grade 4, *etc.* We now have for each person not a preference but a comparison, which is the same thing for this purpose—a comparison between the grade his father was in and the grade in which he is himself. Out of the general complex of comparisons we have to try to build up some kind of measure of the extent to which people as a whole transfer themselves from one grade to another over a period of time, and hence set up some kind of measure of social mobility. Similar problems arise in linguistics, and to some extent, in anthropology, but I shall not elaborate on them. I will, however, mention one point in this preference scheme which is of con-

siderable importance in economics. The older thories of economics tried to set up a theory of price or demand based on what was called "utility" – there was supposed to be in each object some rather mysterious concept called utility, the total of which was maximized by a consumer. Nowadays, we realize that it is not altogether satisfactory to explain something you do know by something you do not – so we try to overcome the difficulty by setting up systems of preference; for example, we suppose that if the consumer is offered varying quantities of two commodities, he will either prefer one to the other, or he will have no preference between them, in which case we can map, as it were, a series of what we call "indifference curves" between his various expenditures at different consumption levels. On the basis of these indifference curves we can set up a theory of demand. The interesting thing about this basis, a point which I think economists overlook, is that if we try to aggregate a set of preferences which are consistent we may arrive at a set which is inconsistent. It is virtually impossible for an individual to prefer A to B, B to C, and still prefer C to A; he doesn't as a rule behave that way. But it is perfectly possible to get a thousand consumers, each of them consistent in his preferences in this sense, who, *on the average*, prefer A to B and B to C, but still, *on the average*, prefer C to A. Thus, certain of the consistency conditions we meet in the basis of demand theory may well not be obeyed; or, if they are obeyed, it is up to the economist to prove it experimentally.

THE ESSENTIALS OF THE STATISTICAL METHOD

Up to this point I have deliberately chosen my examples from as many different branches of science as possible (and perhaps I ought to say that I do not pretend to be an authority on any one of them). It may perhaps have occurred to the reader to wonder what some of these things really have to do with statistics. In the case of the queueing problem, for example, why is this a statistical and not a mathematical problem? If in any system of queueing the service time were constant, and people were arriving and leaving regularly, it is obvious that the problem would be a purely mathematical one. The necessity for discussing the problem statistically arises from the fact that there is some element of chance in the situation. There is an element of randomness in the time of arrival, there is an element of randomness, perhaps, in the time of service for different people, and the differences which one can get between the statistical approach and the purely mathematical approach are sometimes enormous. For example, in the queueing problem, suppose that individuals arrive on the queue once every minute and leave it after service once every minute, it is obvious that the queue will remain constant in size and is, so to speak, under control. But if the arrivals are randomly distributed in time but are at the rate of one a minute, and if the service times are also random but average one a minute, the system is out of control; there will inevitably come a time when the queue is longer than any number you like to think of beforehand. This is a very simple

illustration of the abrupt differences we may get in proceeding from the mathematical case to the statistical case. It is with events which incorporate some elements of chance or randomness in their occurrence that statistics is concerned. Such a chance element can occur in many ways, by the ordinary throwing of dice, as in the gambling problem; in the random walk problem by casual disturbances or arbitrary choices of direction; in the traffic problem by randomness in time; in preference systems by errors on the part of observers, *etc.* Everywhere we are dealing with events which have essentially a chance element in them, and in fact, we have a word for such happenings. Nowadays, we call them stochastic, which is a rather precious way, perhaps, of saying' 'random" or "casual."

When chance is at work in a system, we cannot say anything definite about its behaviour on a single occasion or at a single trial. It is at this stage that we return to the previously mentioned aggregates, because that is where the interest of the statistician lies. Having an experience in dealing with aggregates, and sacrificing the possibility of being certain about behaviour on an individual occasion, he tries to formulate laws of behaviour of collections of occasions. He knows that he cannot predict a single event, but he can and he does successfully predict what will happen in the long run, or in the aggregate, or on the average. Every bridge player, of course, does this, and indeed every individual does a good deal of it for himself in making the decisions of ordinary life. All that the statistician does is to study the necessary procedures intensively, classify them and reduce them to rules. It is, in fact, one of the most peculiar features of modern science that chance, which seems to be conceptually the antithesis of law, is itself reducible to law and can be brought under control and the bringing under control is the main task of the statistician. It is his job to explore the extent and nature of chance variation, and wherever possible, to reduce it; or if he cannot reduce it, to measure it, to gauge its extent on the average, and hence, to bring it under control

This statement, if it is correct, explains why the statistician is led to take part in the development of pure mathematics on the one hand and the development of scientific inference on the other. In mathematics he has, in a sense, invented a new complexity in mathematics. In fact, ordinary mathematics deals with a variable, and the mathematical variable is distinguished by the characteristic that although it can have certain values, one never thinks of it as having certain values more frequently than other values. In statistics, we deal with a random variable which also may take values in a given range, but is to be conceived of as taking certain values more frequently than others, a fact which we express by saying that it has a distribution function, or a probability distribution, or something of that kind. So that, instead of setting up, as it were, a calculus of mathematical variables, we set up a calculus of distribution functions, and that adds a great deal to the complexity of the mathematics which we have to use in statistical theory. The main difficulties of modern mathematics arise out of limiting processes and the justification of inverting certain limiting processes, such as summation of an infinite series and integration.

In statistics, very briefly, we do not encounter any new type of mathematics, but we do, as it were, import another degree of infinity into the problems by having to speak now of distribution functions instead of mathematical variables. It is true, however, that over the course of the last thirty years, practically every branch of mathematics has been overhauled to meet some statistical requirement. Branches of mathematics, like the theory of symmetric functions, which have been put away in the mathematical lumber room for many years, have all been taken down, dusted, used, and in many cases, elaborated. I think it is fair to say that the requirements of the statistician provide one of the most powerful stimuli in mathematical research, but I also express a personal opinion that statistics is not a branch of mathematics. This is a contentious point, but what I mean by that is that there are in statistics ideas which find no place in mathematics, although they are amenable to mathematical treatment. In one sense, the idea of chance is antithetical to mathematical demonstration, which relies so much on the certainty of its deductions. Statistics relies on certainty of categories and the uncertainty of its individuals, and although it tries to express its ideas within the framework of existing mathematics, conceptually it is, I maintain, not a branch of mathematics. One might, perhaps, say that it is a branch of applied mathematics, just as one can say that the theories of electricity, magnetism, optics and heat, are branches of applied mathematics; but when we really come to apply them, we do not often think of them as such, and when we really come to apply statistics, I don't often think of them as such, either.

I mentioned also, at the other extreme of the scale, that the statistician is interested not only in pure mathematics, but also in uncertain inference, and here he has a very definite role to play because, as I explained, he is thinking all the time in terms of random events, and hence, in terms of probability. He sacrifices all hope of being able to make assertions about the future in terms of deterministic rules, but he does not sacrifice the possibiilty of being able to make statements in probability, and in fact, he does exactly that. Nearly every conclusion we draw in statistics is stated in terms of a certain amount of confidence, but not in terms of certainty. I don't want to appear to take too much credit to the statistician for inventing this idea because certain of the physical scientists arrived at the basic idea for themselves, even perhaps before the statisticians did so. The classical case is the kinetic theory of gases, where the physicist gave up all attempts to try to formulate the laws of motion of each of a set of molecules, but formulated the laws of aggregates of molecules. The same thing happened in the theory of heat; and of course in certain modern developments, like quantum mechanics, where you replace an electron by a wave of probability, a very high degree of statistification has been reached. The idea, however, is essentially the same; one cannot say what is happening on an individual occasion; one can say what is happening on a collection of occasions, and hence, whether one likes it or not, one is a statistician. It was Eddington, I think, who once said that the hero of the nineteenth century would have been the man who could explain gravitation by means of cogwheels. The hero of

the early twentieth century would have been the man who could explain physical laws in terms of mathematics. We have abandoned that approach; the hero of the latter part of the twentieth century is going to be the man who can explain physical behaviour, using that in its general sense, in terms of the laws of probability.

The reader can now, I hope, appreciate how the statistician looks at things; why he takes an interest in so many different fields; why statistics is very far from being a dull subject; why the statistician feels an immense pride in the scope of his weapons, but at the same time an immense humility at their lack of precision.

EXPERIMENTATION

I should like, in conclusion, to emphasize certain aspects of the theory of experimental design. In the old days, the statistician — who was usually an economic statistician — had to take what data he could get and be thankful. It was turned out for him by some other machine; he very rarely was able to get it himself. Nowadays, we are beginning to alter that. Whereas, formerly, a statistician, like a physician, was usually called in when the patient was nearly dead, nowadays, so far as possible, we encourage everybody to call him in before anything is really going wrong with the patient at all. In the old days, the statistician made a gallant effort to deal with the data, and that often got him into disrepute. The statistician had to surround his conclusions with so many safeguards and reservations that he presented the picture which I think is still in many people's minds, the picture of a man who constitutionally cannot make up his mind about anything and under pressure can produce any conclusion you like from the data. Now, you must not shoot the statistician; he was doing his best, having had both hands tied behind his back by being denied the possibility of saying anything about the way in which the data were collected. The point which we endeavour to emphasize so much nowadays is the importance of utilizing the statistician as a consultant at the beginning; and if one does that and has a very clear idea of what one wants him to do, he can in fact set up complicated and delicate systems of experimental design which save an enormous amount of labor, both on his part and on the part of the scientist who carries out the experiment.

My final point is that, great as is the field of application of the theory of experimental design, we are really in one sense only at the beginning of developing what one might call a scientific theory of experimentation. It is a rather paradoxical thing, when one thinks about it, that although we have now three hundred years of extensive experimentation, there is very little systematic, logical, and generally accepted theory of the subject. The statistician has a considerable part to play in the development of such a theory, by studying the nature and extent of experimental error, the extraction of the maximum amount of information, and the minimization of effort required to attain given precision.

SUMMARY

To summarize very briefly: I have tried to show that the statistician, although he is necessarily dealing with numerical data, is not, so to speak, primarily interested in them, except insofar as they are a weapon for handling aggregates. It is in the aggregates that he is interested; he sets up a calculus of aggregates; he expresses his thoughts in terms of aggregates, through the medium of probability; in particular he has a contribution to make towards the study and control of error; and since error arises wherever measurement is made there is in practically every scientific field a place for the statistician.

Sex Factors and Selection in Experimental Populations, With a Note on Selection and the Sex Ratio

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Modern biologists generally agree that the generalization most responsible for the tremendous advances in biology in the past three-quarters of a century is the theory of evolution. In retrospect the influence of Darwin's work seems truly amazing when it is realized that two of its central theses rested in his time on exceedingly weak grounds. Darwin and his colleagues were very vague on the question of how new hereditary variation arose. They were even in total error in their concepts of how this variation could spread once it appeared, since they believed essentially that when two variants were crossed the result was a blending of the inheritance contributed by each. Admittedly, the other fundamental proposition of evolution, natural selection, was based even in Darwin's time on a considerable body of indirect evidence. This consisted mainly of inference from plant and animal morphology, distribution, and natural history. Since Darwin these lines of evidence have been further strengthened and a beginning made to correlate them with the principles of genetics (see especially the monographs of Dobzhansky, 1941, Mayr, 1942, and Simpson, 1949, and the mathematical studies of Fisher, 1930, and Wright, 1931). Experimental demonstration of natural selection, however, has been scant. Similarly, there has been little study of the problem's quantitative aspects, such as measurements of the intensity of the selective process. Considerable progress in eliminating this deficiency has recently been made by Dobzhansky and his colleagues in studying chromosomal variants of *Drosophila* of the *obscura* group (subgenus *Sophophora*) in population cages. The work has been reviewed by Dobzhansky (1947 and 1949). It has demonstrated that natural selection could be studied in the laboratory, often duplicating observations in the field, and that the intensity of the process was often much greater than had theretofore been imagined. Using similar methods, the writer found that certain chromosomal variants of the Eastern woods species *Drosophila robusta* Sturtevant (subgenus *Drosophila*) also showed large differences in selective value (Levitan, 1951a). In one of these experiments a further study was made to determine at which period of the life cycle selection occurred. The present paper reports the results of this study together with a re-examination of the experiment in the light of the new data. Data are also presented concerning the stage of the life cycle responsible for the unusual preponderance of females noted in the populations. As these data are presented they will be used to describe many of the theoretical bases for this field of experimental biology and to show how the conclusions drawn often carry implications reaching into many aspects of genetics and evolution.

MATERIAL AND METHODS

The equipment and procedure used in the population cage study were essentially those described by Wright and Dobzhansky (1946) and modified for *D. robusta* by Levitan (1951a). The population mainly to be discussed here, No. 4, involves competition between carriers of two gene arrangements of the left arm of the second chromosome, 2L and 2L-1, for a common food supply. These arrangements, which differ by a one-step inversion of approximately the middle third of the arm, are described by Carson and Stalker (1947). The experiment was begun September 23, 1948, with 878 flies, half of each sex, representing 12 strains of each arrangement (each strain descended from a single fly collected in the New York City area by the author). The initial chromosomal constitution was estimated as 81.3% 2L and 18.7% 2L-1. During the first generation the cage was in a 25° C. room with variable humidity, but thereafter it was kept in an incubator maintained at 25° C. and 89-92% humidity at Columbia University, New York. On September 8, 1949, during the ninth generation, the cage and its contents were moved to Virginia Polytechnic Institute, Blacksburg, and maintained under similar conditions there from September 17 to the present.

Sampling of generation 16 was delayed about two weeks, so that most or all of the eggs and larvae present were the offspring of that generation. The adults were then removed, counted, placed in a new cage, and an egg sample taken from them. The food cups from the original cage were attached to stoppered glass cylinders of the same diameter with tape. These were kept in the same incubator. Flies hatching in the cylinders were collected at five day intervals, aged five to seven days (males and females separately), and mated individually to flies known to be homozygous for 2L. Salivary glands of eight larvae from each cross were smeared in acetocarmine and their chromosomes examined.

Another cage, No. 16, was intended as a study of arrangements 2L and 2L-3 (also described by Carson and Stalker, 1947). An undetected opening into the cage allowed contamination, during both the parental and F_1 generations, by *Drosophila melanogaster*. This accident proved fortunate in making possible two additional counts of hatching *D. robusta* for comparison with the mature adult populations. Flies hatching from the cups outside the cage were collected as with No. 4, but in this case the newly-hatched *D. robusta* were returned to the cage immediately after being counted.

RESULTS AND ANALYSIS

Table 1 shows the results of sampling the eggs laid by population No. 4 for seventeen generations. The data show rapid, directional changes in arrangement frequencies in this cage until the eighth generation. During this period the frequency of 2L dropped to less than half its initial value, 2L-1 showing a concomitant rise. Thereafter, directional changes appear to be absent, the samples showing only apparently random fluctuations about an equilibrium of approximately 35% 2L and 65% 2L-1.

Wright (1931) discusses four possibe causes of changes in frequencies of genetic variables in a population, namely, mutation, selection, migration, and chance factors in the reproductive process (genetic drift). Only selection offers a possible explanation for the changes observed here. Migration was, of course, impossible. The changes were too rapid to have been caused by mutation, and their directional character makes genetic drift extremely unlikely. Wright showed further that the simplest explanation for selective changes which lead to equilibrium is that the heterozygotes are adaptively superior to either homozygote, the point of equilibrium being determined by the relative adaptive values of the homozygotes. In such a case he has demonstrated (in Wright and Dobzhansky, 1946) that the regression coefficients calculated from the regression of frequency changes with time are expressions of the average selective disadvantages of the homozygotes relative to the heterozygotes. Taking the average adaptive value (W) of the heterozygotes to be 1.00, the adaptive values of the homozygous types would also be 1.00 if they had no selective disadvantage relative to the heterozygotes. When the homozygotes are selectively inferior, their W's are 1.00 minus their respective selection (regression) coefficients. Using Wright's method for calculating the selection coefficients (*loc. cit.*) it is found that for the data as a whole:

GENOTYPE	W		
2L/2L	0.35	$s = 0.65$	
2L/2L-1	1.00		$\hat{q}_{2L} = 0.350$
2L-1/2L-1	0.65	$t = 0.35$	

The selection coefficients of 2L/2L and 2L-1/2L-1 are called "s" and "t", respectively. The biological meaning is this: if the heterozygotes in the population are taken to leave 1.00 descendants reative to their numbers in each generation, then the 2L / 2L leave, relatively speaking, "1 — s" descendants, and the 2L-1/2L-1 leave "1 — t". The quantity "$\hat{q}$" represents the equilibrium frequency of 2L that would be expected from these selection coefficients; it can be easily shown that, with minor error, this is equal to $\frac{t}{s+t}$. Although the calculated "$\hat{q}$" appears consistent with the equilibrium actually attained, inclusion of data from eight samples after equilibrium was reached might seem to influence this result. Also, the change in the first generation occurred at different humidity. Re-calculating from only the data F1 through F8, the following is obtained:

GENOTYPE	W		
2L/2L	0.23	$s = .077$	
2L/2L-1	1.00		$\hat{q}_{2L} = 0.364$
2L-1/2L-1	0.56	$t = .0.44$	

Although the relative adaptive values are different, the indicated equilibrium value is again similar to the one obtained experimentally. This set of adaptive values fits the data better than the first set. Under neither set would the equilibrium be expected as early as it was attained, apparently because the method of calculation assumes that the adaptive values are constant. It is more likely that the average adaptive value of the heterozygotes increases slightly during the course of the experiment, as in the data of Dobzhansky and Levene (1951).

Hardy (1908) and Weinberg (1908) independently made a substantial contribution to the study of populations of sexually reproducing organisms. They demonstrated that if there was random mating (panmixia) in a large population in which the frequency of a genetic variant was equal in the gametes of both sexes, the frequency of homozygotes for the variant would be the square of the frequency of the variant itself. Heterozygotes of two allelic variants would have a frequency equal to twice the product of the variant frequencies. Thus in a population consisting of only the chromosomal variants 2L and 2L-1, if the frequency of 2L in both sexes is "q", the frequency of 2L-1 "1 − q", then under random mating the population will consist of

$$q^2 \ \ 2L/2L \ : \ 2q(1-q) \ \ 2L/2L-1 \ : \ (1-q)^2 \ \ 2L-1/2L-1.$$

In the absence of changes either in the relative proportions of the variants or in the mating character of the population, these proportions of the genotypes will remain constant; hence, they are commonly called the Hardy-Weinberg equilibrium frequencies.These theoretical considerations may be used to detect the stage in the life cycle at which natural selection is acting. If it is known that that a population of zygotes consists of the Hardy-Weinberg proportions of the genotypes, it may be inferred that it was formed by random combination of gametes. If no changes in these proportions occur between fertilization and adulthood, the Hardy-Weinberg equilibrium should also be found among the adults. In the population cage cups, if such changes do occur, differential survival of the genotypes between egg and adult stages must be responsible. On the other hand, the absence of such changes would not necessarily indicate the absence of selective forces. Factors such as differential fertility, sexual activity, or longevity among the genotypes are not detectable by this method, unless they caused wide disparity between the frequencies of the variants in the gametes of males and females (and even then would not ordinarily be distinguishable from other factors that can disturb the Hardy-Weinberg formula in egg samples).

The zygotic frequencies of the egg samples in Table 1 were analyzed for consistency with the Hardy-Weinberg equilibrium by means of the Chi^2 test, each sample having one degree of freedom. Fifteen of the seventeen samples do not depart significantly from the expectation under random mating; the deviations in F_3 and F_{15} are slightly significant (Chi-squares of 4.515 and 3.860, respectively, for each of which P is between .02 and .05). The data as a whole, however, have a chi-square of 27.861 for 17 degrees of freedom, which is slightly significant (P between .04

TABLE 1.—Zygotic and Gametic Frequencies (in per cent) of Egg Samples from Population 4. All samples consisted of 150 individuals (300 chromosomes).

Sample	Zygotic Frequencies			Gametic Frequencies	
	2L 2L	2L 2L-1	2L-1 2L-1	2L	2L-1
P (Estimate)	——	——	——	81.3	18.7
P_1 (Sample)	57.3	40.0	2.7	77.3	22.7
F_1	54.7	36.0	9.3	72.7	27.3†
F_2	26.7	55.3	18.0	54.3	45.7*
F_3	21.3	58.7	20.0	50.7	49.3
F_4	16.7	57.3	26.0	45.3	54.7
F_5	18.0	52.7	29.3	44.3	55.7
F_6	16.0	52.7	31.3	42.3	57.7
F_7	15.3	40.7	44.0	35.7	64.3
F_8	12.0	42.7	45.3	33.3	66.7
F_9	——	——	——	——	——
F_{10}	16.7	51.3	32.0	42.3	57.7**
F_{11}	7.3	48.7	44.0	31.7	68.3
F_{12}	6.7	44.7	48.7	29.0	71.0
F_{13}	13.3	50.7	36.0	38.7	61.3
F_{14}	10.7	46.7	42.7	34.0	66.0
F_{15}	12.7	56.0	31.3	40.7	59.3
F_{16}	10.0	53.0	36.7	36.7	63.3
F_{17}	10.7	50.0	39.3	35.7	64.3

* First sample in the high humidity incubator
** First sample in Virginia
† Initial sample for the high humidity experiment

and .05). Furthermore, under random mating the frequency of heterozygotes is never expected to exceed 50%, yet this figure is exceeded in more than half of the samples (9 out of 17). In five other samples the frequency of heterozygotes is in excess of expectation, in only three is it below the expectation. If chance alone were responsible, there should be an excess of homozygotes as often as of heterozygotes. The deviation from this expectation for 17 samples is 2.7 times its standard error, giving a P value of about .01. Apparently the egg samples deviate slightly in favor of the heterozygotes. This may be due to slight departures from panmixia, it may be the result of differential egg mortality, or it may arise from differing frequencies of the arrangementes in the gametes of males and females. If the last-named factor were responsible an excess of

heterozygotes would be expected among the zygotes without reflecting necessarily any adaptive superiority of this genotype. The average excess of heterozygotes in the egg samples is 3.45 ± 0.83 per hundred individuals, each homozygote being deficient by 1.73 ± 0.48 per cent.

TABLE 2.—Frequencies and Relative Survival Values of the Genotypes in F16 Adult Samples.*

	a	a_c	e	e_c	W_s	W_s*
Males	106					
2L / 2L	11	10.80	12.92	11.09	.768	.963
2L / 2L-1	52	52.42	48.18	51.84	1.000	1.000
2L-1 / 2L-1	43	42.78	44.90	43.07	.876	.982
Females	107					
2L / 2L	5	4.76	11.91	10.06	.307	.392
2L / 2L-1	61	61.88	47.58	51.27	1.000	1.000
2L-1 / 2L-1	41	40.36	47.51	45.66	.653	.732
Total Adults	213					
2L / 2L	16	15.56	24.69	21.01	.529	.670
2L-1 / 2L	113	113.91	95.66	103.00	1.000	1.000
2L-1 / 2L-1	84	83.53	92.66	88.98	.757	.849

* See text for explanation of symbols.

Table 2 shows the results obtained from the analysis of adults of generation 17, cage No. 4, that hatched outside the cage and were mated to 2L / 2L flies. The classification of homozygotes, made when all examined offspring had identical genotypes, was generally based on eight larvae; one female 2L-1 / 2L-1 was based on seven, and one male 2L-1 / 2L-1 on six. By this technique some heterozygotes are by chance misclassified as homozygotes. The probability of this error depends not only

on the number of larvae examined but also on the relative probabilities of heterozygotes and each homozygote. Correcting for this error gives the "a_e" values of the table. The Hardy-Weinberg proportions calculated from the arrangement frequencies in each sample, using the a_e values, are listed as "e" in the table. These would be the expected values representing no differential survival between egg and adult stages were the egg samples in concordance with the Hardy formula. Since the egg sample showed a slight excess of heterozygotes and deficiency of homozygotes, the expected values for no differential survival may be similarly corrected, using for this the averages noted at the end of the previous paragraph; the resultant values are called "e_e" in the table. The arrangement frequencies among the adults, 33.2% 2L in the females and 34.9% 2L in the males, are consistent with the equilibrium frequencies suggested by the egg samples (Table 1) and by the adaptive values calculated above. The chi-square test indicates that the differences between the observed and expected zygotic data for the females are probably not attributable to sampling error. This holds true whether the "e" or "e_e" values are used, P being less than .01 or between .01 or .02, respectively. For the male sample the differences are not statistically significant (P may be as low as .30 or as high as .90). For the complete adult sample the differences are of only border-line significance (P about .07), unless the discrepancies from panmixia may be neglected (P less than .01 on the basis of "e").

Relative survival values of the genotypes may be calculated from the data. According to the Hardy formula, the relative proportion of 2L/2L to 2L/2L-1 in an adult sample should be $q/2(1-q)$. Taking the survival value of the heterozygotes to be 1.00, then the observed proportion of 2L/2L : 2L/2L-1 divided by the expected ratio of the two, $q/2(1-q)$, gives the relative survival value of the 2L / 2L. Similar considerations apply for 2L-1 / 2L-1. The homozygote survival value is equal to that of the heterozygotes when the ratio of the two follows the Hardy formula, greater when the observed ratio is larger than the expected ratio, smaller when the expected ratio is larger than the observed ratio. The survival values shown in Table 2 were calculated on the basis both of "e" (W_s) and "e_e" (W_s^*). In all cases the heterozygotes appear to have superior survival value. Considering sampling errors and possible fluctuation in adaptive value not considered in the regression calculations, the survival values of the females are rather similar to the adaptive values of the genotypes calculated from the changes in the population cage. This may well mean that all or most of the female contribution to the overall adaptive values is accounted for by the noted differential survival of the female carriers of these genotypes between egg and adult stages. On the other hand, differential survival, if it occurs at all among the males, cannot account for their contribution to the overall adaptive values, since the resultant adaptive values (given in the table for the total adult sample) are completely different from the ones that apparently were responsible for the changes in the cage. Apparently, natural selection acts in the males at other stages of the life cycle.

The author (Levitan, 1951a) noted that counts of mature populations in the cages invariably gave sex ratios with a high significant preponderance of females. Two of the counts of the older mature adult (P_1 and F_1 of No. 16) and a hitherto unpublished count (F_{16} of cage 4, the parent population of the adults studied above) are given in Table 3. All three counts of the mature flies show the typical excess of females. Comparison of these counts with those of newly hatched flies from the same populations shows clearly that the sexes hatch from the puparia in approximately equal numbers, but the females have a higher survival value during the imaginal stage.

TABLE 3.—Counts of Mature Adult Populations and Their Newly-emerged Offspring in Two Experiments

Population	Cage	Approximate Generation	Total	Females Percent	Males Percent
Initial Adults	16	P_1*	1000	50.0	50.0
Mature Adults	16	P_1**	361	71.7	28.3
Offspring	16	F_1	1273	57.1	42.9
Mature Adults	16	F_1	393	74.6	25.4
Offspring	16	F_2	844	58.8	41.2
Mature Adults	4	F_{16}	437	86.7	13.3
Offspring***	4	F_{17}	537	53.3	46.7

* Upon introduction into the cage.

** Count began 29 days later; contained a few newly-hatched F_1.

*** Offspring in cylinders only (see text); offspring in the cage (eggs sampled as F_{17} of Table 1) not counted.

DISCUSSION

It has been demonstrated here that even during a period of equilibrium the carriers of various genotypes do not have equal selective value. This supports the conclusion of the writer (Levitan, 1951a) that in *D. robusta* also the chromosomal polymorphism is adaptive. Furthermore, the finding that the heterozygotes are the most viable type, at least in the females, lends support to the hypothesis that maintenance of the polymorphism depend on the adapive superiority of the heterozygotes. This allows the polymorphism to exist in spite of the apparent adaptive weakness of some of the genotypes in certain environments and in certain portions of their life cycle (Levitan 1950, 1951a). Paradoxically, the retention of adaptively weak genotypes is of adaptive value to the species, because it gives it increased evolutionary plasticity. The "weaklings" of one environment may be just the ones needed to successfully exploit a new environment.

This study indicates that the evolutionary plasticity of the species may also be increased by adaptive differences between the sexes. In the text

it was shown that only female carriers of the genotypes studied differed in viability. The males were probably also not adaptively equal, but their differences involved some other stage(s) of the life cycle. Likewise, the overall adaptive values were probably different in the two sexes. The writer has also found selectional differences between the sexes in this species in nature (Levitan, 1951a and 1951b). In *D. pseudoobscura*, Wright and Dobzhansky (1946) state that their data from experimental populations were consistent with a hypothesis of large selective differences between the sexes. Later Dobzhansky (1950) found that the relative viability of male and female carriers of chromosomal variants was not always the same; in one of nine studies reported these differences were as extreme as the ones found here. Working with the arrangements of the "sex-ratio" condition in *D. pseudoobscura*, Wallace (1948) demonstrated that males and females differed in adaptive value at a number of stages in the life cycle. Similarly, selective mating which discriminates against mutant males but not against mutant females was found to be the cause of extinction of the gene for white eyes in populations of *D. melanogaster* containing its wild-type allele (Reed and Reed, 1950). Since Wallace and the Reeds were working with sex-linked conditions, however, their results are not strictly comparable to the data in this paper. For sex-linked conditions, males and females differ in gene dosage. Muller (1950a) presents evidence that genes present in single dose have weaker action than in double dose. Also, the increasing evidence that dominance is rarely complete (see citations and discussion by Muller, 1950b and 1950c) makes it questionable, even on genetic grounds alone, whether males hemizygous for a sex-linked dominant and females heterozygous for it present identical phenotypes for natural selection. In the present study, on the other hand, the genotypes of males and females should be identical with respect to the gene arrangements used (and the same holds for the data of Dobzhansky cited above). Nevertheless, there was considerable difference in the action of natural selection upon them. This may be the result of differences in the interaction of sex-linked modifiers with the genes included in these arrangements in the two sexes; or phenotypic differences may have arisen from the interaction of these genes with different extra-genic internal environments in males and females, analogous to the "sex-influenced" genes known in many animals (e.g., the gene for "pattern baldness" in man, which apparently causes baldness in males heterozygous for it, but not in such females (Gates, 1946)). The possibility exists also that the males and females with the same genotypes are phenotypically similar but meet different external environments. At first glance this seems hardly likely in a population cage, but there is evidence, for example, that the pH in a cage cup becomes progressively lower and that more males than females (as larvae and pupae) meet the more acid conditions.

It is well-known that under typical laboratory culture conditions more female *Drosophila* hatch from the puparia than do males. Thus, in their control counts Reed and Reed (1950) obtained 46.8% males and 54.2% females among 25,906 flies, the deviation from a 50:50 ratio being highly

significant. The females develop faster and therefore tend to exploit the available food supply better. One would expect an accentuation of this tendency in a population cup, where literally tens of thousands of larvae must compete for a food supply adequate to allow, at maximum, two or three hundred adults to emerge. The newly hatched populations of cage No. 16 (Table 3) conform to this expectation. On the other hand, the sex ratio does not deviate significantly from 50:50 among the flies hatching from the cups of cage No. 4. The cage 4 data thus reflect a lesser survival value of the females during preimaginal stages, perhaps related to the selection pressure against several female genotypes during this period noted in the text. Taken together with the observed differential mortality favoring the females during the adult stage, these results show that natural selection not only affects the sex ratio but also may influence it in different directions at different points in the life cycle. They call to mind yet another hypothesis of Darwin that has been the subject of little experimental study. Noting the many reports of animals (including man) with higher proportions of males at birth ("secondary sex ratio") but with greater mortality of males thereafter, so that females become proportionally more frequent in the adult (or tertiary) sex ratio, he suggested (1871) that for these species it would be a selective advantage to develop inherited mechanisms insuring that more males are born than females. Thus, selection favoring one sex at one stage of the life cycle would compensate for selection favoring the other sex at a different stage of the life cycle. Some evidence for this hypothesis does exist from studies of chicken mortality by Asmundson (1941). He found that in chickens most of the embryos dying during the last week of incubation were females. Nevetherless, the secondary sex ratio showed an excess of females, because a higher proportion of the embryos dying *before* the last week were males. How general the phenomenon might be remains questionable, however, for in the same author's work with turkeys, selection seemed to favor females throughout the embryonic period.

With respect to man, the significant excess of males at birth has generally been regarded as resulting from a discrepancy from the expected 50:50 ratio at conception (primary sex ratio). The argument has stemmed mainly from several studies of sex ratios among stillbirths (references in Stern, 1949, and McKeown and Lowe, 1951). These data have generally shown highly significant excesses of male stillborn embryos for every month of pregnancy for which data are available. Thus selection seems to favor females in the embryonic period as well as later. As Stern (1949) remarks: "Only if the greater weakness of the male sex were replaced in the earliest period by a greater weakness of the female sex, would the primary ratio be closer to equality than the ratio at two months of prenatal life. Such reversal of the relative mortality of the two sexes is most unlikely." Actually, such a flat statement of the case does not seem justified. For one thing there has been an increasing tendency to question whether the ones which can be examined ar truly representative of all embryonic deaths, particularly since the largest proportion of all embryonic losses probably occur prior to or shortly after implantation and

can, therefore, rarely be examined (McKeown and Lowe, 1951). Also, the census data, which are the basis for many of the reports, have been criticizd by many authors because the identifications as to sex were made by physicians and midwives, who are not particularly expert in identifying the sexes of early embryos. An additional factor which seems to have been overlooked in these discussions is that a greater number of males among the older stillbirths need not indicate a greater rate of mortality of males in these months of pregnancy; it may be only a manifestation of the already greater population of males present because of a greater rate of mortality of female embryos in the early months. For when two numbers are reduced by the same fraction, their ratio to one another remains constant. The relative uniformity of the stillbirth ratios in the later months seems to support this idea. As with so many other genetical problems of man and larger animals, it is likely that further progress on the sex ratio problem must await more evidence and suggestions of lines of attack from work with lower organisms, such as the populations of flies described in this paper.

SUMMARY

Experimental populations of *Drosophila robusta* differing in certain chromosomal arrangements yield quantitative evidence concerning natural selection. Selection appears to favor heterozygotes for the arrangements studied. In one population, the selection process in the females seems to consist of differential mortality between the egg and adult stages, whereas, the selection process in the males apparently occurs at a different stage of the life cycle. It is shown, for several populations, that a high excess of females among the adults is not primarily traceable to the eclosion sex ratio, but is, instead, the result of differential mortality favoring the females during the adult period. Possible genetic explanations for selective differences betwen the two sexes are outlined, and the present status of selectional explanations for variability in the sex ratio is discussed.

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Energy Dissipation in Vibrating Solids[1]

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During the last 15 years or so, the study of energy dissipation in vibrating bodies has proved to be a very valuable technique for investigation of atomic and molecular deformation processes and for elucidating the mechanism of such processes. It is well known that freely vibrating bodies, such as a swinging pendulum, once set into motion will oscillate with a continually decreasing amplitude. Mechanical energy is thus gradually converted into heat energy. It might be expected that this decrease in amplitude, or loss of energy, is due to air resistance or to dissipation of energy at the supports. If the vibration takes place, however, in an evacuated space, and if every precaution is taken to eliminate or reduce as far as possible the energy transmitted to the supports, it is noted that the vibration still dies down in time. This dying down of amplitude, this capability of dissipating mechanical energy, is attributed to a property of the material itself, sometimes called damping capacity or internal friction. This property is a very significant one from the viewpoint of design. A material with large inherent damping capacity is better able to resist operation in the range of its own resonant frequencies than a material of low damping. It is for this reason that low carbon mild steels are frequently used in preference to higher strength alloy steels in some alternating load applications. It is not our intention here to dwell on the design significance of damping or internal friction measurements. Foppl (1936) and others have discussed this point at some length, and the importance of internal energy dissipation or damping under vibrational conditions is now well recognized by the design engineer.

MECHANISMS OF ENERGY DISSIPATION

Of great interest are the underlying mechanisms which are responsible for the conversion of mechanical energy into heat. Through the work of many researchers, of whom Zener (1948) has been one of the most prominent, it is now known that internal damping, or energy dissipation in vibrating solids, is very sensitive to structure and may arise from many different causes. Some of the important sources of energy dissipation are:

1) So called *thermoelastic damping* which may be of macroscopic or microscopic origin. It arises essentially from the fact that different parts of the vibrating object are at different stress intensities, and hence, the local temperatures vary, a temperature gradient exists, and irreversible heat flow takes place. Even if the average macroscopic stress is maintained constant across the specimen cross section, the actual stress intensities at different points will vary because of the random orientation of the

[1] Address delivered at the Scholars' Convocation, Randolph-Macon College, Ashland, Virginia on the occasion of the dedication of Smithey Hall, October 23, 1953.

individual crystallites and of their inherent anisotropies. The theory of damping due to thermal currents has been fairly well established by Zener and his co-workers, and the agreement with experimental evidence is excellent provided the amplitudes of motion are kept small.

2) Damping due to *stress-induced diffusion.* This type of energy dissipation occurs only in solid solutions and arises because application of stress biases the normal diffusion processes that take place. As a result, the material is characterized by a relaxation time corresponding to attainment of equilibrium conditions; a non-elastic component of strain accompanies application of applied stress; a hysteresis loop is present; and mechanical energy appears as heat. A great deal of information concerning the mechanism of diffusion itself can be obtained from studies of vibrational damping of alloys. Such tests can be carried out at room temperatures, whereas conventional diffusion experiments require much higher temperatures in order to get a measurable amount of diffusion. This means that the effect on diffusion of other variables such as number of vacancies, amount of cold work, *etc.*, which are themselves affected by temperature, can effectively be best studied by vibration damping methods of the type now being discussed. For interstitial solutions, a theory has been developed and is in good agreement with experimental data. For substitutional solutions, no adequate theory is yet available (LeClaire, 1953).

3) Damping due to *slip at grain boundaries.* This type of damping occurs only in polycrystalline materials but can be found even in pure materials where stress-induced diffusion damping is absent. The process has been intensively studied by Ke (1947), Pearson (1951), and others but there is as yet no satisfactory theory of the phenomenon which agrees with the experimental results.

4) Damping due to *plastic flow.* This type of damping arises essentially because the stress-strain curve of the material in question is nonlinear. Under alternating loading, a hysteresis loop is present, and energy is dissipated. Present evidence indicates that damping due to plastic flow is possible not only at engineering stresses where plastic behavior is to be expected, but also in some instances at very low strains or stresses where normally one would expect the material to be perfectly elastic. It is reportedly due to oscillatory motion of dislocations which are present in all materials but the precise mechanism is still not clear. The effect of various variables on the measured energy dissipation such as annealing, cold working, age hardening, *etc.* are easily studied by conventional methods and considerable information has been accumulated. As has been noted by Read (1940), Nowick (1953), and others, damping due to plastic flow is usually strongly dependent upon amplitude, whereas all three of the types discussed above, *viz.*, thermal damping, diffusion damping, and grain boundary slip are all independent of amplitude but strongly dependent upon frequency.

5) Damping by *scattering of lattice waves.* This type of damping is significant only at very high frequencies in the megacycle region. The theory for this effect has been given by Mason (1947), who shows, by

analogy with the Rayleigh method for scattering of sound waves from inhomogeneities in gases, that the energy dissipation should vary with the 4th power of the frequency and the 3rd power of the grain size. This dependence has also been found experimentally.

6) *Viscoelastic damping.* This type of energy dissipation is analogous to viscosity losses in fluids and seems to be much more important in non-metallic solids such as high polymers or plastics. Various types of viscous models (Alfrey, 1948) such as the Maxwell Solid in which the deformation accompanying loading is irrecoverable and the Voight Solid, where the strain approaches a constant value asymptotically with time and recovers slowly on removal of the load, have been proposed to account for the observed losses. In general, it is found that the simpler models do not apply to the actual behavior of the solid and more complicated mechanisms have to be propounded.

METHODS OF MEASUREMENT

Let us set aside now this interesting aspect of mechanism and consider how one goes about measuring experimentally the inherent ability of materials to dissipate vibrational energy. This is not so easy to do as one might expect and the literature on the subject (Boulanger, 1949) is notable for the wide discrepancies in the reported values of damping. A direct measure of damping is the reduction in amplitude of a freely vibrating body. This reduction is usually expressed in terms of what is called the logarithmic decrement δ, which by definition is simply the log of the ratio of two successive amplitudes. To a first approximation this is the same as the fractional loss in amplitude per cycle or as 1/2 the fractional loss in energy per cycle. It is not uncommon to find reported values of δ for the same material varying by a factor of 10^3. It is also not uncommon to find great discrepancies in the reported variations of damping with amplitude, frequency, or temperature.

The discrepancies are due largely to three factors:

1) The presence of extraneous and unwanted losses such as acoustical losses and support losses. The first of these is easy to eliminate but the second is much more difficult, especially for low damping materials. One of the usual methods is to support the specimen by wire loops situated at the nodes. Another method (Brennan, 1953) developed in our laboratory at The Pennsylvania State University for use in the study of longitudinal vibrations of rods and tubes is to support the specimen on transverse reeds tuned to oscillate at the same frequency as the natural longitudinal frequency of the specimen. In this manner losses due to friction are kept very small and if necessary can be accounted for and separately determined.

2) Sensitivity of damping to structure and to past history of specimen. This sensitivity is frequently so great that the desired effect is masked by slight changes in structure and in method of handling or treating the specimen. For accurate and reproducible results therefore, the metallurgical structure and prior treatment must be rigidly controlled.

3) The presence of different mechanisms of energy dissipation in different frequency ranges. As mentioned before there are various possible causes for the conversion of mechanical energy of vibration into heat and these mechanisms do not necessarily possess the same amplitude or frequency dependence. Therefore the results of investigations made in different frequency regions can not be directly compared.

Once the appropriate precautions have been taken to avoid extraneous energy losses, there are still various methods that may be used to measure th inherent damping capacity. Which method is used will depend partly on the frequency range which it is desired to investigate. Some of the commonly used methods are:

a) Measure of the decay in amplitude in free vibrations. Results are usually reported in terms of a log decrement and have been obtained using longitudinal vibrations in rods, torsional oscillations of pendulums, and transverse oscillations of simple supported beams or cantilever reeds

b) Measure of the resonance curve in forced vibrations. These forced vibrations may be induced mechanically, electromagnetically, piezoelectrically, or magnetostrictively, and the resultant strain detected in like manner. Usually one records the ratio of the width of the resonance curve at half amplitude to the resonant frequency, and this ratio $\frac{\Delta F}{F}$ can be shown to be directly proportional to the log decrement and to the fractional energy loss per cycle, provided the damping is small.

c) Measure of energy dissipation in forced vibration. This can be done by measuring the rate of temperature rise in the specimen during the forced oscillation or by determining the resonant amplitude and from this calculating the energy loss. The damping is usually expressed in terms of the ratio of the energy loss per cycle $\triangle W$ to the maximum energy W and it can be shown that $\triangle W/W$ in forced vibrations is the same as twice the log decrement in free vibrations provided damping is small.

d) Measure of attenuation in wave propagation. This is particularly suitable for very high frequencies. Provided damping is small, the attenuation constant can be expressed in terms of the fractional energy loss per cycle or in terms of the log decrement.

BRIEF REVIEW OF DATA

The data on internal friction is far too extensive to review adequately in any one lecture. Some of the significant findings are as follows:

1) Measured values of δ are of the order of

10^{-6} for quartz

10^{-3} to 10^{-5} for metals

10^{-2} to 10^{-3} for glass

10^{-1} to 10^{-2} for high polymers

These are only approximate values but the general trend of increasing

the energy absorption ability as we go from the highly crystalline materials to the amorphous or polymeric substances is significant.

2) In many instances, the experimental investigation reveals a peak in the δ vs. T curve, or the δ vs. f curve. This would indicate that some type of anelastic mechanism is present and that some atomic or thermal rearrangement characterized by some relaxation time is taking place. In these cases, it is usually expected δ will be independent of of amplitude though in many experiments the question of amplitude dependence has not been investigated.

3) In other instances, the investigator finds little or no frequency dependence but a noticeable dependence on amplitude. This would appear to indicate a form of hysteresis loss due to plastic flow or essential non-linearity in the stress-strain curve. It is believed to be due to the motion of dislocations but there is as yet no valid theory of the phenomenon.

4) It seems clear that internal energy dissipation in vibrating solids is not viscous in character since ordinary viscosity leads to a direct dependence on frequency for a Voight Model and an inverse dependence upon frequency for a Maxwell Model, and neither is obtained experimentally A more complicated model, usually referred to as a "Standard Linear Solid" and characterized by having some parameter such as the anelastic strain (ϵ_{an}) approach equilibrium in exponential fashion $\epsilon_{an} = \epsilon^{o}_{an} (1 - e^{-t/\tau})$ does lead to a frequency dependence of the energy dissipation of the form.

$$\delta = C \frac{\omega \tau}{1 + \omega^2 \tau^2}$$

where C and ϵ°_{an} are constants, ω is the frequency, t the time, and τ the time of relaxation. This relation is approximated by the observed behavior of some materials--especially at low stress amplitudes where amplitude dependence is not generally found. Qualitatively what happens in such a system is the following: if the frequency is very high, internal rearrangements do not have time to take place; no anelastic strain is produced, and no hysteresis occurs. On the other hand, if the frequency is very low, the system is essentially in equilibrium at each stress; the strain is in phase with stress; and no hysteresis develops. For intermediate frequencies, where the period of oscillation is comparable to the relaxation time, there is an appreciable amount of anelastci strain present, and mechanical energy is dissipated as heat.

5) The effect of annealing on energy dissipation is exactly reversed depending on whether one is considering low amplitude internal friction or high amplitude internal friction. For low amplitudes, appealing reduces δ presumably because dislocations diffuse out in the annealing process; in the high amplitude case, annealing increases δ and cold work decreases δ. Here it is thought that work hardening increases the elastic action of the material and reduces the amount of plastic flow, thus decreasing the size of the hysteresis loop.

RECENT AND CURRENT RESEARCH AT PENNSYLVANIA STATE UNIVERSITY

A number of different research projects in this general field of energy dissipation of vibrating solids have been underway at this University in recent years. They include:

1) Development of an apparatus to produce high stresses at audio-frequencies. Heretofore, all measurements at high stresses have been made at low (mechanical) frequencies and all measurements at high frequencies have been at low stresses. In our newly developed apparatus, a stress range from 100 psi to 7,000 psi has been studied. For aluminum alloys, it has been noted that, throughout this large stress range, the value of damping remains very small ($\delta \sim 10^{-5}$) and there is a noticeable dependence of damping on amplitude (Sauer and Brennan, 1953). The dependence on amplitude was found to be very similar to that observed in a previous low frequency investigation (Sauer *et al.*, 1949) in which a mechanical resonant oscillator was used. Additional features of the Pennsylvania State University longitudinal apparatus are: losses at the supports can be separately determined and accounted for if necessary, and the losses are themselves kept very small by making the supports out of resonant reeds tuned to oscillate at the same frequency as the natural longitudinal frequency of the specimen.

2) By means of a transverse vibration method, the dependence of δ on temperature for a group of high polymers in the lower audio-frequencies is being explored. Some tests have been run at liquid air temperatures and it is expected that much lower temperatures will be reached in the near future. There is some indication from preliminary unpublished work done at the Research Laboratories of the Imperial Chemical Industries in England that resonant peaks may be present in these low temperature regions.

3) Velocity and attenuation measurements are being made in the frequency range of 100 kc. to 1 megacycle using barium titanite transducers and a pulse technique. The critical region in which λ is comparable to the dimensions of the bar, and for which no theoretical solution for the propagation velocity exists is being explored.

4) The contribution to damping caused by finite thermal conductivity has been investigated theoretically (Lessen and Duke, 1953) for the case where the path for heat flow is not fixed but is itself a function of frequency. A single equation for propagation of a stress disturbance has been obtained; for the isotropic case it can be shown that a shear wave is undamped but that the medium is dispersive to longitudinal vibrations as different components propagate at different velocities and hence the wave form is not preserved. It can also be shown that the effect of frequency (ω), is the same as the effect of thermal conductivity (K) i.e. as $K \to \infty$ or $\omega \to \infty$ one gets the isothermal solution and as $K \to 0$ or $\omega \to 0$ one gets the adiabatic solution.

5) An attempt (Sauer and Oliphant, 1949) has been made to introduce damping capacity data as well as fatigue data into the mechanics of

design of resonant members. This study shows that in such applications materials of lower fatigue strength may be more suitable because of higher inherent damping than materials of high fatigue strength.

CONCLUSIONS

Much useful information both for the engineer and the physicist results from studies of energy dissipation in vibrating solids. Some of the benefits accruing from such studies are:

1) Needed information for engineering design purposes is provided, especially for design of resonant members in which damping is more important than strength.

2) More accurate values of the diffusion constant in solid solutions have been obtained and over a much greater range of temperature than was heretofore possible by conventional diffusion measurements alone; activation energies for the responsible mechanism can be estimated; the role played by vacancies in diffusion processes can be studied; and the mechanism of precipitation can be made more definite.

3) Knowledge of grain boundary movements, or activation energy for grain boundary slip, and of effect of impurities can be deduced.

4) The part played by dislocations and lattice imperfections in plastic flow can be investigated. For exampe, it can be shown that dislocations must be of at least two types: one responsible for hardness, the other for internal friction effects. This conclusion is deduced from the fact that the measured value of the energy dissipated can be greatly affected by heat treating and annealing operations that have almost no effect on hardness.

5) An understanding is gradually being developed of the underlying mechanisms responsible for the energy loss and for the atomic and thermal rearrangements that are involved. There are, however, still many unexplored questions and much work needs to be done, both of an experimental and theoretical nature, before energy dissipation in vibrating solids can be said to be a well established and well understood branch of physics.

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The Distribution of Poisonous Snakes in Virginia

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Reported here are records showing the distribution of venomous snakes in Virginia. Prior to 1940 there was only incidental mention of poisonous snakes in this State.[1] In 1940 Gloyd was only able to verify six specific localities in Virginia where timber rattlesnakes had been collected, and the distribution of the cane-brake rattlesnake was based on Brady's (1927) heresay report. Presumably on the basis of specimens, Gloyd and Conant (1943) reported copperheads in 12 localities and cottonmouth moccasins in two. Subsequently a number of reports[2] specify localities in Virginia where poisonous snakes have been observed or collected. These reports have not been summarized previously, and little is known of the distribution of poisonous snakes in Virginia. This accounts for the recent erroneous reports that rattlesnakes are rare in Virginia (Roper, 1951), and that Virginia has only three native poisonous snakes (Taylor, 1952).

Schmidt and Davis (1941) list five venomous snakes in Virginia, as follows: northern copperhead, *Ancistrodon contortrix mokeson* (Daudin); southern copperhead, *Ancistrodon contortrix contortrix* Linnaeus; cottonmouth moccasin, *Ancistrodon piscivorus piscivorus* Lacepede; timber rattlesnake, *Crotalus horridus horridus* Linnaeus; and cane-brake rattlesnake, *Crotalus horridus atricaudatus* Latreille. Gloyd and Conant (1943) failed to find typical southern copperheads in Virginia, and indicated that these snakes in the southeastern counties are actually intergrades between the northern and southern subspecies. With this single alteration in the above list, the above species constitute our native poisonous snakes.

Two other venomous snakes are frequently reported in Virginia. The coral snake, *Micrurus fulvius fulvius* Linnaeus, was erroneously reported as a native species by Barringer (1892). No coral snakes have been collected or observed in Virginia by herpetologists, and none are in museum collections. Barringer undoubtedly made the common mistake of regarding the "false coral" or scarlet king snake, *Lampropeltis elapsoides virginiana* Blanchard, as the dangerous species. The eastern diamond-back rattlesnake, *Crotalus adamanteus* Beauvois, was listed as a possible member of the Dismal Swamp fauna by Brady (1927) but he saw no specimens. Neither of these snakes is known north of the lowlands near Albemarle Sound, North Carolina.

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[1] The following contain incidental mention of Virginia poisonous snakes: Barringer, 1892; Blane, 1824; Brady, 1927; Ditmars, 1935; Dunn, 1915-a, b, c and 1918; Gloyd, 1934; Lynn, 1936; Medden, 1931; Rochefoucault, 1800; Spooner, 1793; Uhler, Cottam, and Clarke, 1939.

[2] Recent literature listing localities where poisonous snakes have been found in Virginia include: Anon., 1953; Clarke, 1953; Goodwin, 1951; Hoffman, 1945 and 1953; Smyth, 1949; and Werler and McCallion, 1951.

The distribution of Virginia poisonous snakes is considered on the basis of the faunal zones defined by Clark and Clark (1951), Map 1. The Coastal Section, consisting of Princess Anne and Norfolk counties, has not been distinguished from the Lower Austral zone because the venomous snake faunae in these two areas are identical. The faunal zones (Map 1) are as follows:

1. Coastal Section and Lower Austral occupy the southeastern counties including part of Gloucester, most of the lower York-James peninsula, and all of the region south of the James River and east of the fall line;
2. Upper Austral consists of the Piedmont, the upper Coastal Plain including the eastern shore counties, the floors of the valleys in the northwestern counties, and the majority of Lee County in the southwestern corner of the state;
3. Transition zone includes the highlands and mountains of the Blue Ridge and Appalachians between 1,500 and 4,000 feet elevation in the north, and 2,000 and 4,500 feet in the south;
4. Canadian zone includes elevations above the limits of the Transition zone, and consists of a few mountain tops in Augusta, Grayson, Highland, Montgomery, and Washington counties.

The distribution of Virginia poisonous snakes has been mapped from data from four sources, including literature records, museum specimens, herpetologists' and naturalists' observations, and medical records of locations where snake-bite accidents have taken place.

Museums and private collections provided 91 locality records based on preserved material including data on 75 copperheads, 7 cottonmouth moccasins, 21 timber rattlesnakes, and 8 cane-brake rattlesnakes. In the locality lists the identity of the sources of the data are indicated with initials and catalog numbers of specimens. The initials of museums and private collections, and the institutions or persons they identify, are as follows:

AMNH—American Museum of Natural History; **ART**—A. R. Turner, Portsmouth, Va.; **CAS**—Chicago Academy of Science; **CM**—Carnegie Museum; **CMNH**—Chicago Museum of Natural History; **JAF**—J. A. Fowler, Philadelphia, Penn.; **JTW**—J. T. Wood, Williamsburg, Va.; **MCZ**—Museum of Comparative Zoology; **OKG**—O. K. Goodwin, Warwick, Va.; **RFC**—R. F. Clarke, Emporia, Kansas; **SNP**—Shenandoah National Park collection, Luray, Va.; **UMMZ**—University of Michigan Museum of Zoology; **USNM**—United States National Museum.

Herpetologists and naturalists reported 295 poisonous snakes from 236 localities. Their reports included locality data giving the distribution of 128 copperheads, 20 cottonmouths, 124 timber rattlesnakes, and 23 cane-brake rattlesnakes. The identity of these observers is indicated in the locality lists by initials with punctuation, and not followed by numbers. All of these observers provided incidental data including dates of observations, character of habitats, and in some cases, behavior and natural history observations. The initials, names, and addresses of the observers are as follows:

A.R.T.—A. R. Turner, Portsmouth, Va.; **C.C.S.**—C. C. Steirly, Waverly, Va.; **C.H.S.**—C. H. Shaffer, Lynchburg, Va.; **C.P.G.**—C. P. Gilchrist, Tappahannock, Va.; **E.D.H.**—E. D. Harris, Norfolk, Va.; **E.V.R.**—E. V. Richards, Keezletown, Va.; **G.B.P.M.**—G. B. P. Mullin, Roanoke, Va.; **H.G.M.J.**—H. G. M. Jopson, Bridgewater, Va.; **H.S.H.**—H. S. Hedges, Charlottesville, Va.; **J.W.E.**—J. W. Engle, Staunton, Va.; **O.K.G.**—O. K. Goodwin, Warwick, Va.; **P.J.H.**—P. J. Hanlon, Harrisonburg, Va.; **P.G.F.**—P. G. Favour, Luray, Va.; **P.M.P.**—P. M. Patterson, Hollins, Va.; **P.R.B.**—P. R. Burch, Radford, Va.; **P.W.S.**—P. W. Sundheimer, Roanoke, Va.; **R.C.**—Roger Conant, Philadelphia, Penn.; **R.F.C.**—R. F. Clarke, Emporia, Kan.; **R.H.C.**—R. H. Cross, Roanoke, Va.; **R.H.M.**—R. H. Manville, Lansing, Mich.; **R.H.R.**—R. H. Rageot, Norfolk, Va.; **R.J.B.**—R. J. Bartholomew, Portsmouth, Va.; **V.D.M.**—V. D. McManus, Williamsburg, Va.; **W.G.L.**—W. G. Lord, Roanoke, Va.; **W.H.M.**—W. H. Massmann, Gloucester Point, Va.; **W.L.B.**—W. L. Burger, Champaign, Ill.; **W.M.W.**—W. M. Wallenborn, Charlottesville, Va.; **W.P.B.**—W. P. Blackwell, Orange, Va.

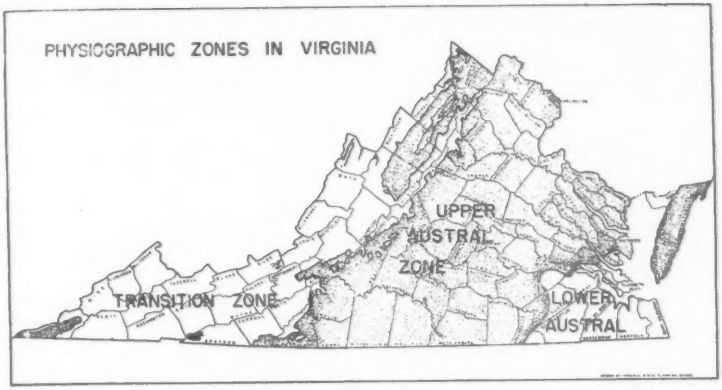
Medical records of snake-bite accidents have contributed 116 locality records to this survey. These include records of bites by 101 copperheads, 12 timber rattlesnakes, two cane-brake rattlesnakes, and one cottonmouth moccasin. In the lists of snake-bite accident locations the initial of the hospital and record number of the case are cited after the locality is listed. The initials of hospitals and clinics, followed by the name and address of each institution, are as follows:

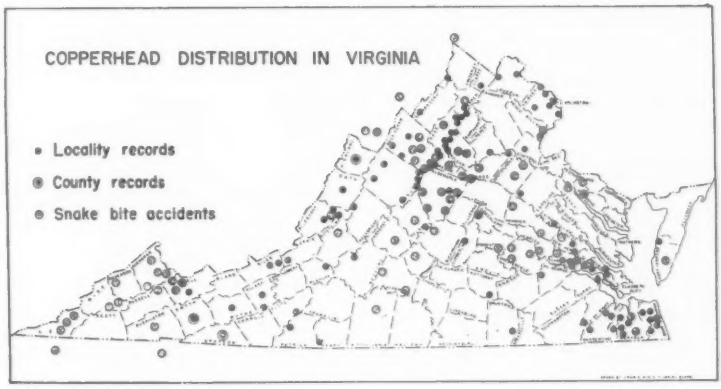
BH—Bell Hospital, Williamsburg; **C-OH**—Chesapeake and Ohio Hospital, Clifton Forge; **CVCH**—Clinch Valley Clinic Hospital, Richlands; **DePH**—DePaul Hospital, Norfolk; **GCH**—Gordonsville Community Hospital, Gordonsville; **JMH**—Johnston Memorial Hospital, Abingdon; **LGH**—Lee General Hospital, Pennington Gap; **LyGH**—Lynchburg General Hospital, Lynchburg; **MCV**—Medical College of Virginia Hospitals, Richmond; **MJH**—Martha Jefferson Hospital, Charlottesville; **MWH**—Mary Washington Hospital, Fredericksburg; **N-AMH**—Northampton-Accomack Memorial Hospital, Nassawaddox; **NGH**—Norfolk General Hospital, Norfolk; **RMH**—Rockingham Memorial Hospital, Harrisonburg; **SBMNH**—Susan B. Miller Nursing Home, Woodstock; **StMH**—St. Mary's Hospital, Norton; **USNH**—United States Naval Hospital, Quantico; **UVH**—University of Virginia Hospital, Charlottesville; **WMH**—Warren Memorial Hospital, Front Royal.

The presence of venomous snakes in Virginia has been mentioned in 31 papers listed at the end of this report. Those including locality data have been used for additional distribution points. All localities based upon published records are followed in the lists by the author's name, and the year the record was published. A total of 522 distribution records have been obtained from sources other than published literature. Together these comprise the basis of the distribution maps.

COPPERHEADS

The vertical distribution of copperheads in Virginia ranges from a few feet above sea level in Princess Anne County to 4,500 feet in the mountain counties. Copperheads are found in all regions of Virginia, but they are unequally distributed through the physiographic provinces. From data compiled in this survey it appears that copperheads are absent in the Canadian zone; uncommon in the higher elevations of the Transition zone, and common on the lower slopes; and widely distributed in all other zones (Upper Austral, Lower Austral, and Coastal Section). Generally they are absent or rare in urban areas, uncommon in suburban areas, and relatively common in rural regions. Most of the museum specimens, literature records, and naturalists observations verify the presence of copperheads in the recreation areas, national and state parks, public forests, and wild regions. Most of the copperhead bites do not take place in these regions, but are recorded where farming and lumbering activities are common, and are frequent near rural dwellings and farms.





MAP 1. (Above). Faunal life zones in Virginia: *Lower Austral* and *Coastal Section* in the southeastern counties; *Upper Austral* in the stippled areas; *Transition Zone* in the western and southwestern counties; and *Canadian Zone* in the solid black areas in the Transition Zone. (After Clark and Clark, 1951).

MAP 2. (Below). The distribution of copperheads and snake bite accidents caused by copperheads in Virginia and its extra-limital areas.

As Roper (1951) pointed out, copperheads appear to be common in Virginia. They are locally abundant in the following mountain counties: Alleghany (Hoffman, 1945), Clarke (Dunn, 1915-c), and Nelson (Dunn, 1915-a). A series of 72 specimens were collected in George Washing-

ton National Forest (Uhler, Cottam, and Clarke, 1939). As the result of extensive field work of National Park naturalists they have been found to be locally abundant in areas scattered along the Skyline Drive and the Blue Ridge Parkway (P. G. Favour, personal communication, March 27, 1953; W. G. Lord, personal communication, March 31, 1953). It is probable that copperheads are locally abundant in all mountain counties. The snake-bite records show that copperheads are widely distributed in the Piedmont counties, and they are cited as abundant in Nottoway (Hoffman, 1953) and Stafford (Lynn, 1936). Although they are apparently uncommon in Princess Anne County (Werler and McCallion, 1951), and most of the remaining Coastal Plain, they are the commonest and most widely distributed poisonous snakes in eastern Virginia.

Copperheads are found in all states bordering on Virginia. They are common in the valleys and low slopes of Harlan County, Kentucky (Barbour, 1950), not uncommon near Raleigh, North Carolina (Brimley, 1923), abundant in the mountains and Piedmont of Maryland, while uncommon over most of the Coastal Plain (McCauley, 1945), and they are reported "occasionally found" in at least two West Virginia counties, Randolph (Green, 1937) and Hardy (Wilson and Friddle, 1950).

Copperheads in the mountain counties gather in the vicinity of overwintering "dens" with blacksnakes and timber rattlesnakes during the fall months. According to Dr. P. R. Burch (personal communication, August 14, 1953) "dens" have been found at elevations ranging from 1700 to 4500 feet; in some dens the rattlesnakes considerably outnumber the copperheads. Burch adds, "All dens I have seen have been on wooded mountainsides with southeastern exposures.—(Dens consist) of weathered outcroppings of rock — with deep crevices which permit the snakes to retreat to a considerable depth below the surface." Individuals have been observed lying on sunlit rock ledges in these areas during spring and fall months. It has recently been reported by Finneran (1953) that in some regions females gather at dens in late summer and early fall, presumably near the time of completion of the gestation period. This has not been reported in Virginia.

Copperheads living in the Coastal Plain are reported to overwinter singly (Neill, 1948). An adult female and two young juveniles were discovered in hibernation by Mr. O. K. Goodwin (personal communication, September 15, 1953). Nothing in known of the over-wintering of copperheads in the Piedmont counties.

The duration of the season of activity of copperheads in Virginia has not been well defined from the compiled field observations, but some appreciation of its extent may be obtained from the following reports. In the highlands of Shenandoah National Park copperheads have been seen in the open from April 16 to December 12, but it is uncommon there to find specimens in the field earlier than May, or later than September (P. G. Favour, personal communication — March 27, 1953). The number of specimens observed in October and November is considerably greater than the number seen in April, indicating that the time of retreat into hibernation is more variable than the time of emergence. On the Coastal

Plain copperheads have been found active on October 26 (Roger Conant, personal communication – March 26, 1953) and still in hibernation on March 16 (O. K. Goodwin, personal communication – March 15, 1953).

The mating of copperheads is preceded by a "combat dance" between males (Gloyd, 1934; 1947). This takes place in spring. The period of gestation is completed in the fall; three records indicate that birth of young occurs in September [Nelson County, September 1st (Dunn, 1915-b); Rappahannock County, September 26, and Greene County, September 28 (P. G. Favour, personal communication, March 27, 1953)]. The number of young produced by one female has been reported for two of the broods as six and seven; in the remaining case two gravid females were confined in one cage, and produced a total complement of 12 young on the same day.

From May through September, Virginia copperheads usually remain in concealment by day, and roam or forage at night. When they are exposed in their diurnal retreats they usually vibrate their tails, and briefly remain alert and motionless. They then slowly retreat into other concealment. If injured, molested, or frightened by sudden motions they may strike. They are frequently found in wood piles, slab heaps, and old stone walls. They feed on mice, caterpillars, and shrews (Uhler, Cottam, and Clarke, 1939).

DISTRIBUTION OF COPPERHEADS BY COUNTIES, MAP 2

[188 Localities]

ALBEMARLE: Campbell (UVH-149869); Charlottesville (W.M.W.) (UVH-124771, 356627); Covesville (UVH-354369); Crozet (UVH-243545, 231504); Keswick (UVH-120607); Rio (UVH-77926); Scottsville (MJH-45924, UVH-286214).

ALLEGHANY: Clifton Forge (C-OH 56036); 2 mi. W of Clifton Forge (USNM 127600); 3 mi. N of Clifton Forge (CM 28216); North Mtn., 12 mi. E of Clifton Forge (UMMZ 84321); Little Middle Mtn., 6 mi. N of Clifton Forge (USNM 124781).

AMHERST: Amherst (LyGH-18054, 57957).

APPOMATTOX: Appomattox (LyGH-16691).

ARLINGTON: Between Chain Bridge and Falls Church (USNM 95192).

AUGUSTA: 3 mi. N of Rockfish Gap, SNP (W.M.W.); Calfpasture River (P.J.H.); Horsehead Overlook, SNP (SNP-16); Lithia Spring (USNM 36763); North River (E.V.R.); Sherando Lake area (H.G.M.J., O.K.G.); Stribling Spring (USNM 36780).

BATH: Warm Springs Mtn. (H.G.M.J.).

BEDFORD: Little Stony Creek, BRP (W.G.L.).

BOTETOURT: Eagle Rock (C-OH 59061); North Creek (P.W.S.); Roaring Run Gap (USNM 127650).

BRUNSWICK: 4 mi. E of Brunswick (UMMZ 84319).

BUCHANAN: Council (CVCH-43802); Pilgrim's Knob (CVCH-49590, 64180); Roseann (CVCH-37901, 61992); Whitewood (CVCH-12987, 48001, 62662).

BUCKINGHAM: Manteo (UVH-256846).

CAMPBELL: Brookneal (LyGH-19091); Evington (LyGH-53170).

CAROLINE: Chilesburg (USNM 48876-77).

CHARLES CITY: Holdcroft (MCV-4851); 1.5 mi. W of Chickahominy River Bridge, nr James River (O.K.G.) (JTW-3104); Roxbury (MCV-118675); 4 mi. W of Chickahominy River Bridge, Rt. 5 (JTW-3515); 8 mi. W of Chickahominy River Bridge (J.T.W.).

CHESTERFIELD: Hallsboro (MCV-9901); Richmond (MCV-130398); Winterpock (MCV-86442).

CLARKE: White Horse, 2 mi. above Berry's Ferry (Dunn, 1915-a).

CRAIG: Barbour's Creek (P.W.S.); John's Creek Mtn., near Maggie (P.R.B.).

CULPEPER: Rapidan River (USNM 84151, 84170); Rappahannock River ,1 mi. above jct. with Rapidan R. (H.S.H.).

CUMBERLAND: State Forest (C.H.S.).

DICKENSON: Clintwood (StMH-10347, 10576).

ESSEX: Loretta (MCV-29437).

FAIRFAX: Alexandria (USNM 10374); Dead Run nr Cabin John (USNM 35734); Elkins (USNM 62062); Great Falls (USNM 25817, 49994, 55410); opposite Plummer's Island (USNM 49721); Waples Mill Road (USNM 117559).

FLOYD: Smart View picnic area, BRP (W.G.L.); Mile 157, BRP (W.G.L.).

FRANKLIN: 8 mi. S of Rocky Mt. (C.H.S.).

FREDERICK: Vances Cove, Paddy Run (E.V.R.).

GILES: Mtn. Lake Biological Station (P.M.P., AMNH 69601); 2.3 mi. N of Mtn. Lake Biol. Sta. (CMNH 56496).

GOOCHLAND: Caledonia (UVH-228822).

GRAYSON COUNTY: County record (R.H.C.)

GREENE: Loft Mtn. Overlook, SNP (P.G.F.); Simmons Gap, SNP (P.G.F.); So. River Falls Trail, SNP (P.G.F., R.H.M.); Stanardsville (UVH-254825); Swift Run Gap, SNP (JTW 2332).

HANOVER: Beaverdam (MCV-86671); Mechanicsville (MCV-118511).

HENRICO: Richmond (MCV-4278, 86545, 118077, 130398).

HENRY: Spencer (CM 18085).

HIGHLAND: County record (J.W.E.).

ISLE OF WIGHT: 1 mi. E of Franklin (R.J.B.).

JAMES CITY: Williamsburg (MCV-34023; BH-200303; JTW 2334,3103,3208); 4.5 mi. W of Lee Hall (J.T.W.); Dunbar area, Williamsburg (JTW 895); Lake Matoaka Park, nr Williamsburg (W.L.B.).

KING WILLIAM: Palls P. O. (MCV-91361); Manquin, nr Pamunkey River (W.H.M.; JTW 2714).

LEE: Calvin (LGH-28220); Jonesville (LGH-23467); Pennington Gap (LGH-25497, 30797).

LOUDOUN: Bluemont (USNM 51893); Leesburg (USNM 10361).

MADISON: Graves Mills P. O. (UVH-296935, 358721); Hughes River Gap, SNP (P.G.F.); Madison (UVH-163748) nr Skyland entrance road, Skyline Drive, SNP (P.G.F.); Rapidan River camp, SNP (R.H.M.); Spitler Knob Overlook, SNP (P.G.F.).

MATHEWS: Bayside (NGH-35931).

NANSEMOND: Buckhorn P. O. (R.H.R.); Dismal Swamp (USNM 26263); Lake Prince area (R.F.C.); 2 mi. NW of Suffolk (R.F.C.).

NELSON: Lovingston (UVH-44155, 248610); 40 mi. below Lynchburg on James River (Dunn, 1915-a).

NEW KENT: Quinton (MCV-4819, 4231); Walkers (CM 30691); 5 mi. N of Diascund Bridge (CM 30695).

NORFOLK: near Norfolk (Buckley, 1953); Hickory (DePH-3936); Bowers Hill (ART-59); 1-2 mi. N of Deep Creek (R.F.C.); Hodges Ferry (ART-517); 1 mi. N of Hodges Ferry (R.F.C.); Lake Drummond, E shore (R.J.B.); Lake Drummond, N shore (R.J.B.).

NORTHAMPTON: Jonesville (R.C.); Northampton (N-AMH-2336594).

NOTTOWAY: Camp Pickett (USNM 131925).

ORANGE: Barboursville (GCH-5889); Gordonsville (GCH-7217); Hawfield Farm (W.P.B.); Rapidan (GCH-8726).

PAGE: Bushy Top, SNP (P.G.F.); near Luray (UVH-204338, 204339); Skyland, SNP (AMNH 8594); Thornton Gap, SNP (USNM 59880).

PATRICK: Rock Castle Gorge near Rocky Knob camping area, BRP (W.G.L.).

PITTSYLVANIA: Gretna (LyGH-16982).

POWHATAN: Clayville (MCV-119702).

PRINCE GEORGE: near Petersburg (Anon, 1953).

PRINCE WILLIAM: near Dumfries (JAF-1132); Quantico (USNH-33536).

PRINCESS ANNE: Pungo (ART-514); 3 mi. SW of Pungo (CM 22944-46); West Neck Creek, Pungo Twp. (Werler and McCallion, 1951); 2 1-4 mi. E of Princess Anne (CM 23212); Princess Anne Twp. (Werler and McCallion, 1951); 2 mi. NW of Kempsville (J.T.W.); 4 mi. W of Virginia Beach (Werler and McCallion, 1951).

PULASKI: Towes Ferry, near Newbern (R.P.B.); Radford College Farm (P.R.B.).

RAPPAHANNOCK: Buck Hollow Overlook, SNP (P.G.F.); Elkwallow Gap, SNP (P.G.F.); Hogwallow Flat Overlook, SNP (P.G.F.); entrance to J. Gray Fire Road, SNP (P.G.F.); Rangeview Cabin, SNP (P.G.F.).

RICHMOND: Farmer's Fork (MWH-8950).

ROANOKE: 1-2 mi. S of Hollins (P.M.P.).

ROCKBRIDGE: Arnold's Valley (P.W.S.).

ROCKINGHAM: Big Run Overlook, SNP (RHM-96833); Bridgewater (H.G.M.J.); Broadway (RHM-89741); Briery Branch (H.G.M.J.); 6 mi. N of Grottoes (JTW 3105); Harrisonburg (RMH-67313, 97782); Keezletown (RMH-103599, 121551); Mt. Crawford (RHM-

67196); Rocky Bar, Elkton (RHM-67684); Simmons Gap, SNP (P.G.F.); Singer's Glen (USNM 37784); Swift Run (RMH-81858, 98096).

RUSSELL: Drill (CVCH-14563).

SHENANDOAH: Orkney Springs (USNM 48529).

SMYTH: County record (R.H.C.).

SPOTSYLVANIA: Fredericksburg (MWH-9704); Spotsylvania (MWH-9480).

STAFFORD: Onville, near Aquia Creek (Lynn, 1936).

SURRY: Hog Island (C.P.G.).

TAZEWELL: Amonate P. O. (CVCH-12019); Bandy (CVCH-7966, 25962); Freestone Valley (P.W.S.); Jewell Ridge (CVCH-13806, 21274, 55048); Jewell Valley (CVCH-56002); Raven (CVCH-31765).

WARREN: Mile 9, Skyline Drive, SNP (P.G.F.); Riverton (WMH-3719).

WARWICK (CITY): 2 mi. NW of Lee Hall (JTW 1002).

WASHINGTON: Abingdon (JMH-50585, 51979).

WESTMORELAND: Montross (MCV-68452).

WISE: Esserville (StMH-3101); Wise (StMH-10430).

WYTHE: Iron Mtn. (P.W.S.).

YORK: 9 mi. W of Yorktown, Colonial Parkway (JTW 2333); 1-2 mi. N of Williamsburg, Rt. 60 by-pass (JTW 1493); 1 1-2 mi. E of Williamsburg, Colonial Parkway (JTW 1494).

Abbreviations not mentioned previously:

SNP—Shenandoah National Park; **BRP**—Blue Ridge Parkway.

DISTRIBUTION OF COPPERHEADS (EXTRA-LIMITAL COUNTIES) (MAP 2)

HANCOCK COUNTY, TENNESSEE: Sneedville (LGH-25982). **JOHNSON COUNTY, TENNESSEE:** Mountain City (JMH-47628). **HARDY COUNTY, WEST VIRGINIA:** Petersburg (RMH-90672). **MORGAN COUNTY, WEST VIRGINIA:** Cacapon State Park (J.T.W.). **PENDLETON COUNTY, WEST VIRGINIA:** Cherry Grove (RMH-87754); Franklin (RMH-128130).

COTTONMOUTH MOCCASINS

In Virginia cottonmouth moccasins are confined to the counties south of the James River and east of Petersburg. They are known to be common in a few localities in this range, Map 3, all situated in either Princess Anne or Norfolk counties. They are found in North Carolina counties bordering the region of known their range in Virginia, and are absent from all other extra-limital counties.

Werler and McCallion (1951) report cottonmouths as common near West Neck Creek, Princess Anne County. They are also common in the Northwest River, Norfolk County, and in the vast bayside swamps along the barrier beach, where they are separated from the mainland by a series of brackish bays.

The earliest date on which cottonmouths have been seen in Virginia in the records of this survey is April 26, but they have been observed as late as December 4. Neill (1948) reports that they hibernate late in the year in Georgia; nothing is known of the time of hibernation in Virginia. Several observers have reported migratory behavior of the cottonmouths from the bayside swamps of barrier beach to the mainland in late October and early November. In a period of as little as three or four days as many as 50 specimens have been observed swimming across Back Bay in the vicinity of the wildlife refuge. This seemingly gregarious behavior may be related to the hibernating habits, but to date nothing is known of the over-wintering of this species in Virginia. In Georgia they hibernate singly (Neill, 1948), and in Mississippi during the hiberna-

tion period they are usually found under logs and stumps in the vicinity of their summer habitat (Allen, 1932). They do not appear to overwinter near their summer habitat in the Back Bay region of southeastern Virginia.

During their active season cottonmouths are found in habitats providing a permanent body of water and inaccessibility to man. The water area may be sluggish or still, and is often associated with a bay or swamp. Cottonmouths do not range far from water, and are frequently found sunning on horizontal limbs overhanging the water. From these sites they can drop into the water when they become alarmed. Cottonmouths feed on fish, frogs, turtles, snakes, birds, and small mammals (Parker, 1937); Smith, 1950). Courtship activities and the "combat dance" of this species occur in spring months, probably March and April in Virginia (Carr and Carr, 1942; Smith, 1950).

DISTRIBUTION OF COTTONMOUTH MOCCASINS BY COUNTIES, MAP 3

[25 Localities]

NANSEMOND: 6 1-2 mi. S of Suffolk (R.C.); Cypress Chapel (R.C.); Dismal Swamp (Clarke, 1953).

NORFOLK: 1-2 mi. N of Deep Creek (RFC-62); Lake Drummond (R.F.C.); 5 mi. S of Deep Creek (RFC-17); South Norfolk (E.D.H.); North Landing (R.F.C.); 1-2 mi. W of North Landing (R.C.); Northwest (RFC-614); 1-2 mi. E of Northwest (A.R.T.); 3 mi. NE of Northwest (R.J.B.).

PRINCE GEORGE: Petersburg area (Anon., 1953).

PRINCESS ANNE: Back Bay (H.G.M.J.) (C.H.S.); Barrier beach area (Werler and McCallion, 1951); False Cape, 5 mi. N of state line (CM-22990); Munden (C.P.G.); North Landing (C.P.G.); Princess Anne, 1 mi. E (CM-23215); Princess Anne Twp. (Werler and McCallion, 1951); Sand Bridge (MCZ 45317); Seashore State Park (CM 23620); West Neck Creek, Pungo Twp. (Werler and McCallion, 1951).

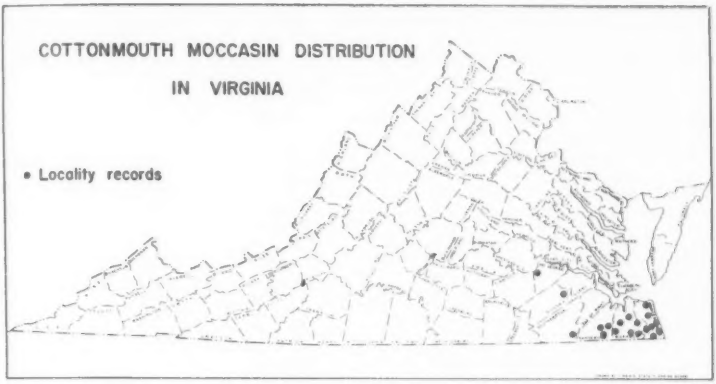
SOUTHAMPTON: 8 mi. S of Franklin (R.J.B.).

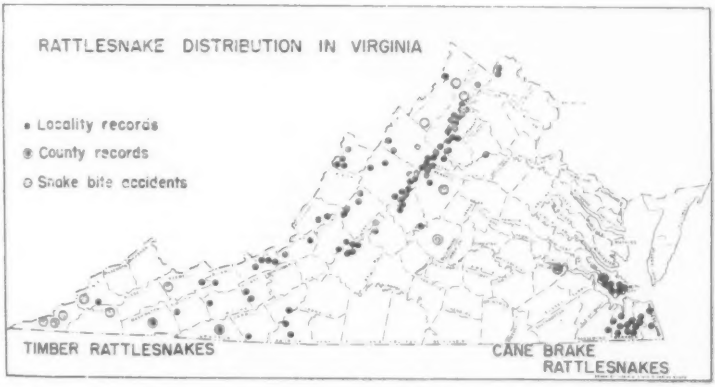
SUSSEX: Coppahaunk Swamp, near Spring Hill (C.C.S.).

CANE-BRAKE RATTLESNAKES

The cane-brake rattlesnakes are confined to the Lower Austral and Coastal Section counties of southeastern Virginia, Map 4. Their range is more extensive than that of the cottonmouth moccasin Map 3) in that they range north of the James River, on the lower York-James peninsula. Although they are probably not numerous in any part of their range, they are not uncommon east of Morrison, Warwick City, where seven specimens were reported killed in a single day during a clearing operation in 1947 (V. D. McManus, personal communication, October 13, 1949). Werler and McCallion (1951) report that although this species is said to range widely in Princess Anne County, they encountered only one specimen in the course of their herpetofaunal survey of that area.

Active cane-brake rattlesnakes are reported in the field from early May through September. One hibernating specimen was discovered and killed on January 26, and another extremely sluggish specimen, presumably found in hibernation, was killed in the field on March 11 (R. J. Bartholomew, personal communication, March 11, 1953). A few late observations have been reported (November 5, and 26), but no data are available





MAP 3. (Above). The distribution of cottonmouth moccasins in Virginia.

MAP 4. (Below). The distribution of rattlesnakes in Virginia: timber rattlesnakes are found in the western and southwestern counties, and cane brake rattlesnakes are in the southeastern counties.

regarding the state of activity of these specimens. Hibernating specimens have been found alone, not in dens that are the familiar over-wintering habitats of the closely-related timber rattlesnakes.

Pope (1944) reports that the largest cane-brake rattlesnake he has examined measured 74 inches in total length. Werler and McCallion (1951) found the longest specimen reported to date from Virginia, a 72 inch specimen found in Princess Anne County. The usual specimen is

considerably smaller, more frequently ranging in total length from three to five feet.

DISTRIBUTION OF CANE-BRAKE RATTLESNAKES BY COUNTIES, MAP 4.

[24 Localities]

HAMPTON (CITY): 6 mi. NW of old Hampton boundary (O.K.G.); 4 mi. NE of Newport News (O.K.G.); near Fox's Store (O.K.G.).

PRINCE GEORGE: Hopewell (MCV-113955).

NANSEMOND: Dismal Swamp (Clarke, 1953).

NORFOLK: Algren (R.F.C.); Benefit (R.J.B.); Craddock, 1 mi. S (ART-54); Deep Creek, 3 mi. S (R.F.C.); Great Bridge (R.F.C.); Hickory, 1 mi. N (R.J.B.); Hickory, 3 mi. S (R.J.B.); Kempsville Road (R.F.C.); Lake Drummond Church (R.F.C.); Stumpy Lake (R.H.R.); Wallaceton (R.F.C.).

PRINCESS ANNE: Pungo (Werler and McCallion, 1951); Stumpy Lake (R.F.C.); Virginia Beach, 3 mi. N (R.F.C.).

WARWICK (CITY): Denbigh area (JTW-3355); Harpersville (O.K.G.); Hilton Village (O.K.G.); Morrison, 1 mi. E (V.D.M.); Morrison, 3 mi. NE (O.K.G.).

TIMBER RATTLESNAKES

The timber rattlesnakes in Virginia are widely distributed over the mountain and valley counties of the western part of the State, where they are largely confined to the Transition zone, Map 4. Their range is well separated from that of the cane-brake rattlesnakes. A local abundance of timber rattlesnakes has been reported in elevated parts of Alleghany (Hoffman, 1945), Giles (Smyth, 1949), and Bedford counties (H. S. Hedges, personal communication, April 23, 1953). Rattlesnakes have been found more common than copperheads on the higher mountain slopes. Carroll (1950) pointed out this distribution in stating that during the summer of 1948 22 timber rattlesnakes were collected in the vicinity of the Mountain Lake Biological Station, Giles County, but that only one copperhead had been taken in the same area during the season. Along Apple Orchard Creek, Bedford County, 50 rattlesnakes were killed in a camping area during the summer of 1933, 40 in 1934, and 9 in 1935. In the course of a food habits survey 141 rattlesnakes were killed in George Washington National Forest (Uhler, Cottam, and Clarke, 1939). Timber rattlesnakes are also found in all highland regions bordering on Virginia. They are found in Bell, Harlan, and Pike counties, Kentucky, and Greenbrier, Hampshire, Morgan, and Pocahontas counties, West Virginia (Gloyd, 1940).

Dens inhabited by timber rattlesnakes have been reported at elevations ranging from 1700 to 4500 feet (P. R. Burch, personal communication, August 14, 1953). The season of activity of these snakes in Virginia extends from the middle of May through September. In Shenandoah National Park the earliest date on which a timber rattlesnake has been seen is April 18, and the latest date, December 7. October and November observations are far more common than those made in April, suggesting that the time of onset of hibernation is more variable, and extends over a longer interval, than the period of emergence from over-wintering.

Smyth (1949) provides evidence to verify the solitary habits of timber rattlesnakes during the summer months in Virginia. It has been noted

that there is a marked increase in the number of rattlesnakes seen along the Blue Ridge Parkway following periods of summer drought (W. G. Lord, personal communication, March 31, 1953). Pope (1946) observes that in the spring and fall timber rattlesnakes may be seen in the open during hours of daylight, but in the summer they remain in concealment by day, and are active at night. The food of these snakes, based upon a survey of the contents of 141 stomachs, includes mice (38 per cent), rabbits (18 per cent), birds (13 percent), and shrews (5 per cent) (Uhler, Cottam, and Clarke, 1939).

DISTRIBUTION OF TIMBER RATTLESNAKES BY COUNTIES, MAP 4

[96 Localities]

ALBEMARLE: Charlottesville (UVH-206789, 66255); Brown's Gap (P.G.F.); Moorman's River (H.S.H.); Patterson Field on Skyline Drive, SNP (P.G.F.).

ALLEGHANY: Richpatch (USNM 127602); 5 mi. S of Covington (USNM 127601); 11 mi. E of Clifton Forge (UMMZ 79428); 12 mi. E of Clifton Forge (CAS 4454).

AMHERST: W slope of Mt. Pleasant (H.S.H.); Blue Ridge Parkway (W.G.L.).

AUGUSTA: Big Levels Refuge (W.P.B.); Crimora Lake Overlook, SNP (P.G.F.); McCormick Gap Overlook, SNP (P.G.F.); Mile 6, Blue Ridge Pky. (W.G.L.); Mile 8.8, Blue Ridge Pky. (W.G.L.); Mile 11, Blue Ridge Pky. (W.G.L.); Sherando Lake area (O.K.G.); Stokesville (H.G.M.J.); Staunton Dam (H.G.M.J.); West Augusta (P.S.H.).

BEDFORD: Blue Ridge Parkway (W.G.L.); Peaks of Otter (W.G.L.); Mile 88, Blue Ridge Pky. (W.G.L.).

BLAND: Freestone Valley (P.W.S.).

BOTETOURT: Apple Orchard (R.H.C.) (H.S.H.); Blue Ridge Parkway (W.G.L.); North Creek (R.H.C.) (P.W.S.).

BUCKINGHAM: County record (Dunn, 1918).

CARROLL: Mile 208, Blue Ridge Pky. (W.G.L.).

CLARKE: White Horse, 2 mi. above Berry's Ferry (Dunn, 1915-c).

CRAIG: Barbour's Creek (R.H.C.) (P.W.S.); John's Creek Mtn., 1 1-2 mi. NW of Simmonsville (CMNH 56498-99); John's Creek Mtn., fire tower near Maggie (P.R.B.).

CULPEPER: Rapidan River (USNM 84149-50).

FLOYD: Mile 169, Blue Ridge Pky. (W.G.L.).

FREDERICK: Middletown (SBMNH 9026).

GILES: Mtn. Lake Biol. Station (Smyth, 1949) (AMNH 71813, 73134, 69251) (P.M.P., P.R.B., W.L.B.) (CM 18513) (CMNH 56497); near Pearisburg (CM 21255); Little Stony Creek, Mtn. Lake Biol. Sta. (P.R.B.); Butt Mtn. (UMMZ 89870).

GRAYSON: County record (R.H.C.).

GREENE: Kinderhook, near South River (AMNH 63832); Simmons Gap, SNP (R.H.M.).

HIGHLAND: Erwin Hollow (P.J.H.); Kent Simmons Hollow (P.J.H.); Upper Campbell Hollow (P.J.H.); 5 mi. W of Monterey (P.R.B.).

LEE: Hubbard Springs (LGH 30321); Jonesville (LGH 12954); Pennington Gap (LGH 30765).

LOUDOUN: Hillsboro (USNM 14755); 3 mi. N of Round Hill (JAF-1053).

MADISON: Hughes River Gap, SNP (P.G.F.); Old Rag Mtn. (O.K.G.); Rapidan River camp, SNP (R.H.M.); near Spitler Knob Overlook, SNP (P.G.F.); near Franklin Cliffs Overlook, SNP (P.G.F.).

NELSON: Mile 29, Blue Ridge Pky. (W.G.L.); Mile 30, Blue Ridge Pky. (W.G.L.); 40 miles below Lynchburg on James River (Dunn, 1915-a).

PAGE: Elkwallow picnic grounds, SNP (P.G.F.); Elkwallow Wayside, SNP (P.G.F.); near Piney River Ranger Station, SNP (P.G.F.); Pinnacles, SNP (P.G.F.); 10 mi. N of Swift Run Gap (W.M.W.).

PATRICK: near Stuart (P.R.B.); Rocky Knob (C.H.S.).

PULASKI: 6 mi. SW of Pulaski (P.R.B.); National Forest (C.H.S.).

RAPPAHANNOCK: Mile 16, Skyline Drive, SNP (P.G.F.); near Pinnacles Overlook, SNP (P.G.F.); Piney River, SNP (R.H.M.); Rangeview area, SNP (P.G.F.); Rattlesnake Point, SNP (P.G.F.); Tunnel Overlook, SNP (P.G.F.); County record (USNM 19920).

ROCKBRIDGE: Arnolds Valley (P.W.S.); Goshen Pass below Laurel Run (H.S.H.).

ROCKINGHAM: Block Hollow, Geo. Wash. Nat. Forest (P.J.H.); Briery Branch (H.G. M.J.); Brown Mtn. Overlook, SNP (P.G.F.); Fulks Run, N of Harrisonburg (H.S.H.); near Big Run fire tower, SNP (P.G.F.); near Rocky Top Overlook, SNP (P.G.F.); 9 mi. S of Elkton (W.M.W.); 1 mi. N of Simmons Gap, SNP (P.G.F.); 5 mi. N of Swift Run Gap, SNP (W.M.W.).

SCOTT: Dungannon (Thomas, 1953).

SHENANDOAH: Newmarket (RMH 97074).

SMYTH: Hurricane Branch, Iron Mtn. (P.W.S.).

TAZEWELL: Big Creek, near Richlands (CVCH 11495); Freestone Valley (P.W.S.).

WARREN: Compton Gap, SNP (R.H.M.); Front Royal (UVH 228060); Lands Run Gap, SNP (P.G.F.).

WASHINGTON: County record (R.H.C.).

WISE: Stonega (LGH 25490); High Knob (P.W.S.).

WYTHE: Iron Mtn. (P.W.S.).

DISTRIBUTION SUMMARY

The distribution of poisonous snakes in Virginia is important to both physicians and laymen. The interest of the physician stems from the fact that copperheads inflict relatively mild cases of venom poisoning, and rattlesnakes generally cause grave cases. If the physician practices in an area inhabited only by copperheads, he can anticipate, with very high probability, a favorable outcome in the case of unidentified snake-bite. The copperhead is the only poisonous snake found in 47 of the 98 Virginia counties, as follows:

ACCOMAC
AMELIA
APPOMATTOX
ARLINGTON
BRUNSWICK
BUCKINGHAM
CAMPBELL
CAROLINE
CHARLES CITY
CHARLOTTE
CHESTERFIELD
CULPEPER
CUMBERLAND
DINWIDDIE
ESSEX
FAIRFAX
FLUVANNA
GLOUCESTER
GOOCHLAND
HALIFAX
HANOVER
HENRICO
HENRY
JAMES CITY
KING AND QUEEN
KING GEORGE
KING WILLIAM
LANCASTER
LOUISA
LUNENBURG
MATHEWS
MECKLENBURG
MIDDLESEX
NEW KENT
NORTHAMPTON
NORTHUMBERLAND
NOTTOWAY
ORANGE
PITTSYLVANIA
POWHATAN
PRINCE EDWARD
PRINCE WILLIAM
RICHMOND
SPOTSYLVANIA
STAFFORD
WESTMORELAND
YORK

Map 5 shows timber rattlesnakes present in Buckingham and the east border of Nelson counties, based upon records more than 35 years old. The present survey has not established that rattlesnakes have persisted in these regions. The Culpeper specimen is fairly recent, non-specific as to locality, and probably originated in the southwestern highlands of the county although other distribution data suggest that rattlesnakes are infrequent in that area today.

In 11 counties the copperhead is widely distributed, and the timber rattlesnake is restricted therein to the vicinity of the foothills and mountains along the western borders. These counties are all along the margin of the merging Piedmont and Blue Ridge, and are as follows:

ALBEMARLE
AMHERST
BEDFORD
FAUQUIER
FRANKLIN
GREENE
LOUDOUN
MADISON
NELSON
PATRICK
RAPPAHANNOCK

In 31 counties both copperheads and timber rattlesnakes are prevalent.

The copperheads predominate in the valleys and lower slopes, and the rattlesnakes in the higher slopes. The counties are as follows:

ALLEGHANY	FREDERICK	RUSSELL
AUGUSTA	GILES	SCOTT
BATH	GRAYSON	SHENANDOAH
BLAND	HIGHLAND	SMYTH
BOTETOURT	LEE	TAZEWELL
BUCHANAN	MONTGOMERY	WARREN
CARROLL	PAGE	WASHINGTON
CLARKE	PULASKI	WISE
CRAIG	ROANOKE	WYTHE
DICKENSON	ROCKBRIDGE	
FLOYD	ROCKINGHAM	

The cane-brake rattlesnakes, cottonmouths, and copperheads are found in 9 counties as follows:

GREENSVILLE	NORFOLK	SOUTHAMPTON
ISLE OF WIGHT	PRINCE GEORGE	SURRY
NANSEMOND	PRINCESS ANNE	SUSSEX

The only poisonous snakes on the eastern end of the York-James peninsula (Hampton, Newport News, and Warwick) are cane-brake rattlesnakes.

ACKNOWLEDGMENT

Records reported in this survey have been contributed by many workers. Museum records were provided by the following curators: Mr. C. M. Bogert, Dr. D. M. Cochran, Mr. W. E. Duellman, Mr. P. G. Favour, Dr. H. K. Gloyd, Dr. A. Loverdge, Mr. C. H. Pope, and Mr. N. D. Richmond. Records of specimens in private collections have been provided by the following herpetologists: Mr. R. F. Clarke, Mr. J. A. Fowler, Mr. O. K. Goodwin, and Mr. A. R. Turner.

Observations have been contributed by the 27 naturalists and herpetologists listed earlier. These workers represented the following institutions: Blue Ridge Parkway, Bridgewater College, George Washington National Forest, Hollins College, Jefferson National Forest, Michigan State College, Philadelphia Zoological Society, Radford College, Shenandoah National Park, University of Illinois, University of Virginia, Virginia Commission of Game and Inland Fisheries, Virginia Division of Forestry, and Virginia Fisheries Laboratory.

Medical records on cases of snake venenation in Virginia were made available by the 19 Virginia hospitals and clinics listed earlier.

Without the generous cooperation of all of these persons and institutions this survey would have been impossible. The author acknowledges his gratitude to all of the above.

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A New Branchiobdellid of the Genus *Cambarincola* (Oligochaeta, Branchiobdellidae) from Virginia [1]

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The branchiobdellid worms, among several other groups of animals, are adapted to a life on the exoskeleton of holoarctic freshwater crayfishes. Available data indicate that this is an obligate relationship on the part of the worms in spite of the fact that there is evidence that most members of the latter are not parasitic on the host. That the relationship is not of recent origin seems probable in view of the fact that certain species are restricted to certain anatomical regions of the crayfish. Some are found on the chelipeds (species of *Xironogitan* and *Xironodrilus*), others around the bases of the pleopods, while a few are restricted to the branchial chambers. The new species described below is found in the latter.

The first branchiobdellid recognized was a gill inhabiting form, *Branchiobdella astaci*, which was described in 1823 by Odier. Subsequent reference to the presence of these worms in the gill chambers of crayfishes are meager but Gruber (1883) reported *B. hexadonta*, an European species, from the branchial cavity of its host, and Yamaguchi (1934: 216) found *Stephanodrilus ezoensis* and *S. megalodentatus* only in the gill chambers of the Japanese crayfishes while *S. inukaii* and *S. nipponicus* were found in the gill chambers as well as on the outer surfaces of the host. *Cambarincola branchiophila*, sp. nov. is the second known North American species which is known to be restricted to the branchial chambers of the crayfish; of the other North American species only *Bdellodrilus illuminatus* (Moore 1894) is confined to this microhabitat.

Cambarincola branchiophila, sp. nov.

(Plate I, figs. 1 to 5)

Diagnosis.——Gill inhabiting branchiobdellid; lips entire, set off by a sulcus from the remainder of the head; dental formula 5/5, with lateral almost teeth longer than teeth between them and median tooth; major annulations not raised; proximal part of the spermatic vesicle bifurcate; accessory sperm tube shorter than spermatic vesicle but relatively large in diameter; spermatheca elongate, spatulate, subequal in diameter throughout its length; medium sized, relatively thick worms, superficially resembling *Bdellodrilus illuminatus* in external appearance.

Description.——Eight specimens, mounted entire, of this species have been studied. The following measurements are those of the type specimen which approaches the maximum in size. Total length: 3.37 mm.

[1] From a thesis submitted to the Graduate Faculty of the University of Virginia in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Diameter, segment I: 0.38 mm. Diameter, segment VI: 0.70 mm. Diameter, sucker: 0.41 mm. Length, head: 0.33 mm. Diameter, head: 0.40 mm.

The general appearance of this worm, when examined with the low power of the dissecting microscope, is quite unlike most members of the genus. In the contracted state, however, it resembles *Bdellodrilus illuminatus*. This resemblance is seen in the relatively great diameter of the sexual segments in comparison to that of the head and sucker – a condition apparently the result of the less heavily muscular character of the anterior and posterior regions – and in the strongly arched form of the body when contracted. This apparent similarity between these worms is superficial for upon careful examination the cambarincolid characteristics of *Cambarincola branchiophila* become evident.

The lips are entire, without indentations, lobes, or tentacles, and are set off from the remainder of the head by a sulcus. The head is further subdivided by another encircling groove, which with the one that sets off the lips, divides the head into three parts (fig. 1). This is in contrast with the condition in *Bdellodrilus illuminatus* where the head is divided into four parts (Moore 1895: 499).

The body outline is, in general, smooth; the major annulations are not significantly raised above the minor ones except at the anterior and posterior ends of contracted animals where they are slightly elevated. The characteristics of the gut, the location of the single nephridiopore, and the location of the anus are similar to those of the other members of the genus.

Although in lateral aspect the jaws appear to be similar to those of *Cambarincola philadelphica*, a critical study of them reveals their distinctive character. The dental formula is 5/5, the dorsal and ventral jaws being similar. The lateral teeth are subequal in length to the median one, while the teeth lying between the lateral teeth and the median one are shorter (figs. 4 and 5).

The reproductive system resembles somewhat that of *C. philadelphica*, but the following differences may be noted. The proximal portion of the spermatic vesicle which receives the vasa deferentia is rather deeply indented or bifurcated between the points of entry of the vasa deferentia. The vasa deferentia are large for the genus, being 22.8 microns in diameter in the type specimen, whereas those of *C. philadelphica* average only 13.1 microns in diameter with 14.2 microns the maximum recorded (Holt, 1949: 552). The spermatic vesicle lies obliquely along the left side of the coelom in the type specimen and gives off the accessory sperm tube and the ejaculatory duct from its anterodorsal border. The size of the accessory sperm tube, 52 microns in diameter in the type specimen, is its most distinctive characteristic; in *C. philadelphica* this diameter averages only 28.2 microns (Holt, 1949: 552-553). A proportionally large bulb terminates the blind end of the accessory sperm tube in *C. branchiophila*. The spermatic vesicle measures 99.8 microns in diameter just distad to the bifurcation mentioned above; in contrast, the spermatic vesicle of *C. philadelphica* averages 82.5 microns in diameter.

The ejaculatory duct is relatively larger in *C. branchiophila* than in *C. philadelphica*. The bursa, while as large, relatively, as in other species studied (Holt, in ms.), appears to have thinner and less muscular walls, particularly in the part which ensheathes the penis, but this is a point that needs to be confined by the study of sectioned material.

The spermatheca (fig. 3) is almost straight, running vertically along the left side of the gut in the type specimen. The spermathecal duct is rather short and the bulbular portion is of not much greater diameter than the duct. The whole is spatulate in outline.

Type locality.—Sinking Creek, Giles County, Virginia.

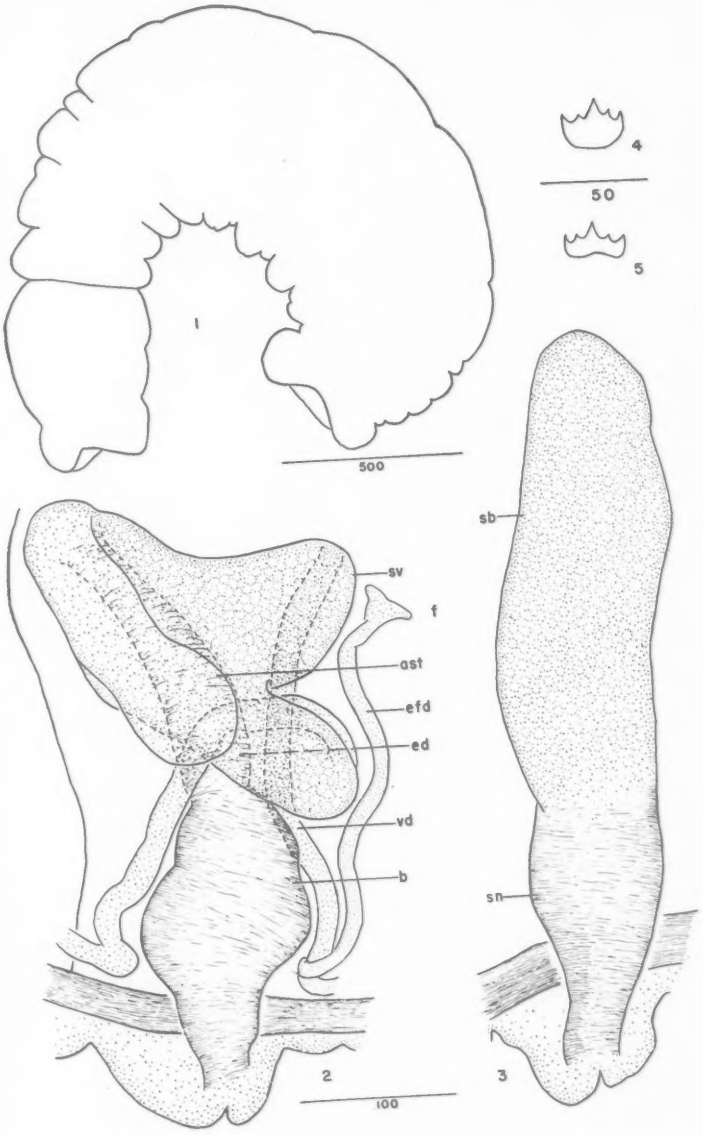
Hosts.—*Cambarus bartonii bartonii* Fab. and *Cambarus sciotensis* Rhoades.

Disposition of types.—The holotype is deposited in the United States National Museum, Cat. No. 25855. One paratype is in the collection of Horton H. Hobbs, Jr., University of Virginia, and the remaining paratypes are in the author's collection.

Specimens examined and locality record.—Eight specimens mounted entire from Sinking Creek, Giles County, Virginia, at the point where crossed by State Highway 700. Collectors: F. D. Kiser, Cornelia Tuten, and P. C. Holt.

Relationships.—*Cambarincola branchiophila* belongs to Goodnight's subgenus *Cambarincola*, but a more exhaustive study must be made of the numerous described and undescribed species of the genus before the validity of Goodnight's subgeneric groupings is confirmed. The dental structure of *C. branchiophila* is, as far as is known, peculiar to this species, approaching in the almost subequal length of the lateral and the median teeth the condition in *C. vitrea*, where the teeth of the upper jaw are subequal (Ellis, 1919: 258), but differing in the dental formula and structure of the lower jaw as well as in the shortness of the next to the most lateral teeth. The male reproductive system, while clearly cambarincolid in character, is not markedly similar to that of any previously described species and resembles most closely that of a new species in the author's collection (Holt, in ms.). It differs noticeably from previously described forms in the greater diameter of the accessory sperm tube in relation to that of the spermatic vesicle and in the bifurcate character of the latter.

Remarks.—This species' adaptations to a habitat not shared, so far as is known, by any of its congeners are worthy of note. The more obvious of these adaptations are the reduction of the body wall musculature mentioned above and an apparent increase in the size and number of the epidermal glands found in all branchiobdellids. Histological studies are needed to confirm the latter. These features—the reduced musculature and the larger epidermal glands—are shared with *Bdellodrilus illuminatus*, and in some unknown fashion would appear to be correlated with the conditions of life in the gill chambers of the host. It is the author's belief that a study of the adaptations of the branchiobdellids to anatomical regions of their hosts should furnish much material for many pleasant hours of speculation by those interested in problems of 'ecological speciation" and convergent, as well as divergent, evolution.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EXPLANATION OF FIGURES

1. *Cambarincola branchiophila* in lateral view.
2. Male reproductive system of *C. branchiophila*.
3. Spermatheca of *C. branchiophila*.
4. Upper jaw of *C. branchiophila*.
5. Lower jaw of *C. branchiophila*.

Legend.——ast, accessory sperm tube; b, bursa; ed, ejaculatory duct; efd, efferent duct; sb, bulb of spermatheca; sn, spermathecal duct; sv, spermatic vesicle; vd, vas deferens.

Changes In The Physiography Of Oyster Bars In The James River, Virginia[1]

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The intent of the Baylor Survey of 1892 was to define the naturally-producing oyster grounds in Virginia waters and to set them aside for public use. Actually, some natural ground was omitted and some barren ground was included within the bounds of the Survey; however, it stands as a definition of public grounds from which any citizen of the State may, for a small fee, obtain a license to take oysters. Only hand tongs are permitted in this public fishery.

These oyster bars within the Baylor Survey are about twice as extensive as the ground outside leased to private planters but they yield only about one-third as many oysters of market size (Marshall, 1951). On the other hand, certain of these public grounds provide the seed or small oysters that are transplanted to private grounds and are essential to the success of leased bottoms which are seldom self-sustaining. Based on this relationship an extensive area in the lower James River (Figure 1) noted for its capacity to produce great numbers of small oysters, has been established by law as a seed area. This area is not subject to the usual regulation that oysters must remain on public grounds till they grow to marketable size. Tongers harvest and sell to private planters from one to two million bushels of seed oysters from this James River area annually. Actually each such bushel is a mixture of small seed oysters, the old shell to which the seed have attached, and a small quantity of oysters of marketable size.

The removal of this mixture of live oysters and shell might reduce critically the amount of cultch available for the setting of larvae. This might also cause decline and other changes in the surface of the bars, thus modifying the hydrodynamics of the region and otherwise disturbing ecological conditions. The widely varied speculations concerning such effects make it especialy imperative to search for data on this subject. A step that can be taken toward this end is to compare soundings on early hydrographic surveys with those taken more recently and thus to observe some of the physiographic changes that have actually occurred. The first complete depth surveys of the portion of the lower James River in question are those made by the U. S. Coast and Geodetic Survey in 1854-55. Additional comprehensive surveys were conducted by the Survey in 1871-73 and 1943-45. All such soundings are plotted on what are known as hydrographic surveys which, of course, provide the primary reference data for drafting navigation charts, *etc.*

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[1] Contribution from the Virginia Fisheries Laboratory, No. 52 Contribution No. 17, Oceanographic Institute, Florida State University.

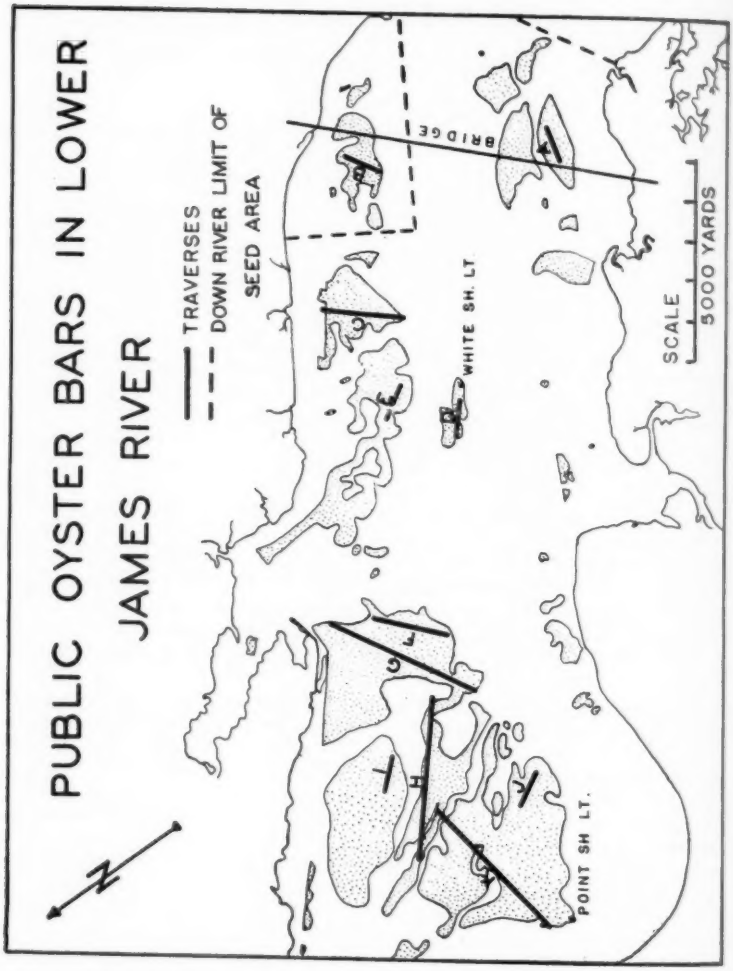

FIGURE I. Public Oyster Bars in Lower James River. The location and length of these traverses, also the names of the bars covered, are indicated in Table I.

METHODS

From Moore's (1910) maps of the oyster grounds in the area, as his party observed them shortly before his publication, traverses were selected across representative bars. Each such traverse (Figure I and Table I[2]) is a straight line, crossing, for at least 75 per cent of its length, grounds which Moore designated as supporting a dense growth of oysters. An exception is the straight line across Brown Shoal which, though not covering such a high percentage of dense growth, was studied to represent bars that were formerly exposed at low water.

These traverses were plotted on the hydrographic survey of each period mentioned above, and using the shortest interval practical on the less intensive older survey, the depths were read every 100 yards. Thus at every hundred yards a point was established at which depths could be compared on successive surveys. As reported by the U. S. Coast and Geodetic Survey (correspondence from the Acting Director, 1949 and 1952) there has been a 0.6 foot rise in sea level in the region between 1855 and the late 1940s. To allow for this in the present study concerned with bottom changes, a one-half foot correction factor was used when comparing soundings of the 1940s with those of earlier years.

The points on these traverses that lie over slopes and channels are not well suited for this study. Oystering is not limited to the crests of the bars, yet points over the slopes often miss oyster bottom; depths at such points are likely to be altered primarily by hydrographic conditions, perhaps with little relation to oystering and oyster growth; and errors in surveying and draftsmanship are exaggerated in contrasts over sloping surfaces. For these reasons, only those points over relatively level stretches of the bottom, well up on the bars, were compared.

RESULTS AND DISCUSSIONS[3]

At 121 of the points compared the bottom was more elevated in the 1850s than it was in the 1940s, whereas the reverse was true at 38 points. An analysis of the depth differences at these points for the entire ninety-year period is as follows:

Number of points compared	= 173
Mean of depth differences	= −1.1 ft.
Standard deviation of differences	= 1.9 ft.
Standard error of differences	= 0.14 ft.
t value	= 7.9
95% fiducial limits of differences	= −0.82 to −1.38 ft.

[2] Point of Shoals Light and White Shoals Light, used as reference points in defining the traverses, are not operating but still stand. In some cases it was obvious that a traverse drafted on Moore's maps of the area crossed slightly different grounds than when plotted on the hydrographic surveys of the U. S. Coast and Geodetic Survey. It was assumed that this was due chiefly to errors in Moore's maps. This does not, of course, affect the accuracy of comparisons between hydrographic surveys.

[3] Table II presents a summary of the data giving means of depths and means of differences at comparison points. The complete data are on file at the Virginia Fisheries Laboratory and are scheduled to appear in the **Proceedings of the National Shellfisheries Association for 1953** (near print).

An analysis of the depth differences for the first 17-18 years is as follows:

Number of points compared	= 173
Mean of depth differences	= −0.3 ft.
Standard deviation of differences	= 2.2 ft.
Standard error of differences	= 0.17 ft.
t value	= 1.8
95% fiducial limits of differences	= +0.04 to −0.64 ft.

As another check, all the depths at the comparison points were lumped for each of the three periods. These three samples were subjected to an analysis to see if they might have been drawn from a single population. This analysis of variance gives an F value of 5.90, indicating a greater than 99% probability that there is a real difference between the groups.

These analyses support certain generalizations, applicable to the extent these data represent the history of the oyster bars. Over the ninety-year span there has been a mean lowering of about one foot from the crests of the bars, this being in addition to the depth change due to a rise in sea level. This figure is statistically significant, far better than the 1% probability level, and lies within relatively narrow fiducial limits. The analysis for the first eighteen years leaves greater doubts as to the validity of the calculated depth change of 0.3 feet. The low t value indicates that the mean difference is not highly significant, and the fiducial limits indicate the change could have been a slight increase rather than a loss from the surface of the bars.

Quite noticeable in survey comparisons is the almost complete disappearance of emergent or intertidal oyster shoals since the 1870s. Though the surveys do not always indicate it, it is probable that the typically elongate, exposed areas in the middle of the oyster grounds are intertidal oyster reefs. Ignoring the shoals adjacent to and thus essentially a part of the shore, approximately 12,000 yards of intertidal reefs were noted from the 1854-55 surveys, 17,000 yards in the 1871-73 surveys, and less than 100 yards in recent surveys. On the original surveys there are so many indications of more thorough work in the 1870s than in the 1850s that the added reef measurements of the second period seem to result from more critical surveying. On the other hand, the difference indicated between the 1870s and the 1940s seems real, as would be expected with a one-foot mean loss from the surfaces of the oyster bars plus the half-foot rise in sea level.

DISCUSSION

The depth comparisons may be discussed under two interdependent headings – the net loss of surface over the ninety-year period, and the variation from point to point. The variation indicates that changes in the bars may be quite different even within relatively short distances. This is also apparent from depth contours, as illustrated in Figure II of the White Shoals area. That the changes should be so varied seems to

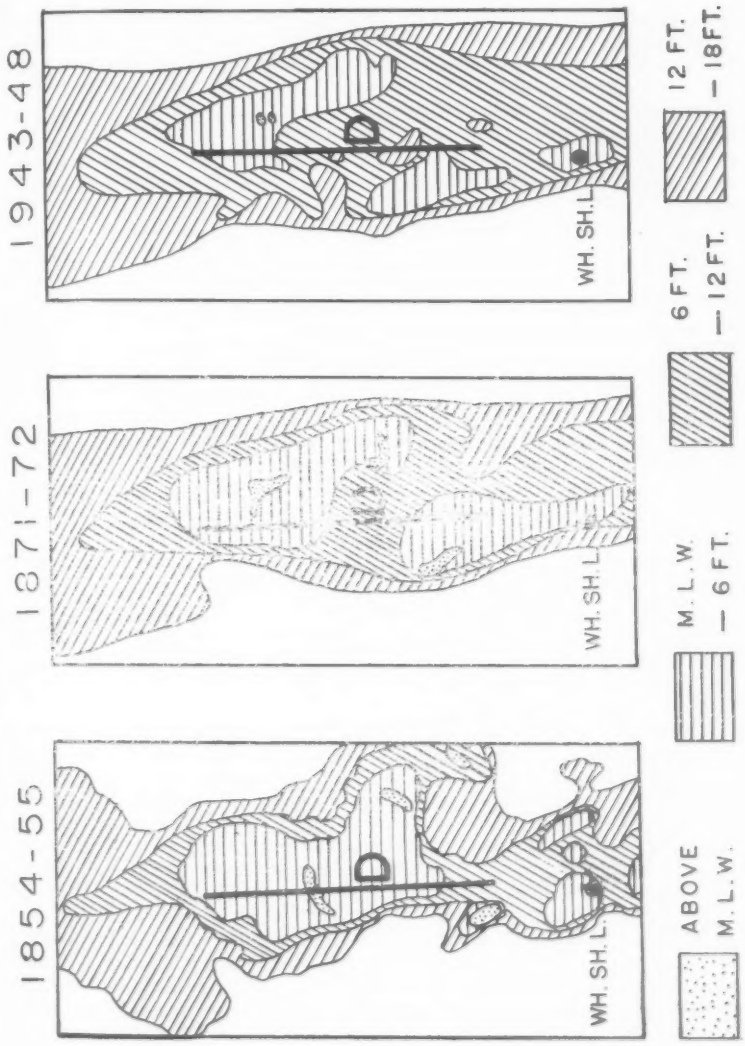

FIGURE II. Depth Contours in the Vicinity of White Shoals Light. Traverse D, 1000 yards, is drawn in to show location and scale.

stress the importance of natural environmental factors, cutting, building, and depositing sediments to mold the shape of the grounds. Thus the bars are quite dynamic, everchanging in form. Though the physical and biological forces involved must be set aside in this discussion as a complex not thoroughly analyzed, it is important to recognize that final effects involve an interaction between such natural forces and the fishery influences. Such interactions are similar to those encountered in dealing with the many fishery populations that obviously vary in response to environmental forces.

Before considering the possible role of the fishery in the net decline of the bars, two forces should be mentioned that constantly tend to lessen the depth. (1) Whatever oysters are on the bars continuously add to their shells and thus to the bottom development. (2) This is an area of salting out of matter in suspension, associated with a marked downstream increase in the salinity and clarity of the water (see Chesapeake Bay Institute Data Report, No. 7, 1952, for tabulations of salinity and light transmission). Brown, Seavy, and Rittenhouse (1939) reported large scale filling due to sedimentation in the York River and Gottschalk (1945) reported the same for the upper Chesapeake Bay and its tributaries. If the James is at all comparable, it must be assumed that there has been a great deal of filling in the seed area. It may be, however, that the scouring and cleansing action of live oysters has kept sedimentation at a minimum over the bars.

To consider the effect of oystering in the over-all decline in the surfaces of the bars it is necessary to estimate the magnitude of shell removal by the fishery. Catch statistics applicable to the seed area, which coincides with the region of these depth comparisons except that the latter included Brown Shoal (Traverse B B[1]), are the only records from which we might estimate shell removal rates. The harvest of seed oysters in Virginia is given in various U. S. Fish and Wildlife Service (formerly U. S. Bureau of Fisheries) reports and is presented in what appear to be comparable summaries for the 1920-21 and the 1924-25 seasons and the years 1929 through 1944. The average annual seed harvest in these years in terms of U. S. standard bushels was 1,675,000. Since only seed oysters are harvested from the James River seed area and since the recorded Virginia seed harvest is almost entirely that of the James, it seems reasonable to use a rounded figure of 1,500,000 bushels to represent the annual removal during the period covered by the data.

The use of the bars in the lower James River has changed through the years, but as Wharton's (1948) historical review suggests, oystering in the state was probably as intensive in the 1850s as it is today and the James River has always been the center of this fishery. Thus the estimate of 1,500,000 bushels a year, taken from the region now defined as a seed area, may be used for the entire period since 1854. Of this harvest the actual volume in seed is small for the small oysters are generally attached to empty shells which may comprise about two-thirds of the total or 1,000,000 bushels annually. On the other hand, removal of empty shell from the surface of bars was undoubtedly less extreme in former years when

the region was used more for market oysters. For an approximation of the average annual removal of empty shell incidental to the removal of live oysters from this area since the 1850s, a figure of 700,000 bushels will be used.

Moore (1910) found about 3200 acres of dense growth on the bars of the present seed area. If we assume that two-thirds of the estimated shell removal comes from such areas this would amount to a layer 0.05 inches deep taken from this area annually. At such a rate a little less than 5 inches of shell would have been removed in the ninety-year period, whereas the net decline at the points compared was about 1 foot.

These removal estimates, being extremely crude, cannot be used as a basis for critical interpretations. On the other hand, if one were to make allowance for factors tending to build the bars and then were to estimate the removal of shell involved in the net loss of a foot, the figure would greatly exceed the above estimates from catch records. This raises many questions. The catch records may fall far short of the actual harvest, or the actual lowering of the bars may be less than indicated by the data presented here. The removal of shell may initiate depletion processes which exceed the amounts tonged from the bars. Possibly there has been some settling of the river bottom in general, producing a lowering of oyster bars.

SUMMARY

This study compares original U. S. Coast and Geodetic Survey depth observations over the productive oyster bars of the lower James River for the period 1854-55 through 1943-48. There was considerable variation in the physiographic changes in the surface of the oyster grounds during that period; however, at most points depth comparisons indicated decline, and the net effect was a mean loss of about a foot in the elevation of the bars.

The variations in depth comparisons and changes in the courses of depth contours suggest that oyster bars are quite dynamic, changing form in response to environmental factors. The physiographic history of these bars is probably the result of both natural and fishery influences just as fishery populations have complex histories of interwoven fishing and environmental effects.

ACKNOWLEDGMENTS

Some of the expense and support for this study has been borne by the Virginia Fisheries Laboratory and the Chesapeake Bay Institute. My former associates at the Virginia Laboratory, Dr. Jay D. Andrews and Dr. J. L. McHugh, have been especially helpful in reviewing this manuscript.

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TABLE I. Location of Traverses of Oyster Bars in the Lower James River, Virginia

GALLEY SIXTEEN (16)			
	Distance	*Direction*	*Reference*	*Traverse Description*
A	5985 yds.	30.2° EofS	of Wh. Shoal Lt.	1000 yds. across
A[1]	6795 yds.	35.6° EofS	of Wh. Shoal Lt.	Fishing Pt. Rks.
B	6350 yds.	81.9° EofS	of Wh. Shoal Lt.	1000 yds. across
B[1]	5539 yds.	76.0° EofS	of Wh. Shoal Lt.	Brown Shoal
C	2168 yds.	87.9° EofN	of Wh. Shoal Lt.	2000 yds. across
C[1]	3818 yds.	65.3° EofN	of Wh. Shoal Lt.	Kettle Hole Rk.
D	1328 yds.	45.6°WofN	of Wh. Shoal Lt.	1000 yds. across
D[1]	315 yds.	42.5°WofN	of Wh. Shoal Lt.	White Shoal
E	2025 yds.	12.3° EofN	of Wh. Shoal Lt.	1000 yds. across
E[1]	1455 yds.	40.2° EofN	of Wh. Shoal Lt.	Thomas Pt. Rk.
F	9030 yds.	86.4° EofS	of Pt. Shoal Lt.	2000 yds. across
F[1]	7680 yds.	75.9° EofS	of Pt. Shoal Lt.	Wreck Shoal
G	6210 yds.	75.7° EofS	of Pt. Shoal Lt.	4000 yds. across
G[1]	7585 yds.	87.8° EofN	of Pt. Shoal Lt.	Wreck Shoal
H	4058 yds.	58.9° EofN	of Pt. Shoal Lt.	4000 yds. across
H[1]	6488 yds.	84.3° EofS	of Pt. Shoal Lt.	Mulberry Swash Rk.
I	5640 yds.	70.8° EofN	of Pt. Shoal Lt.	1000 yds. across
I[1]	6010 yds.	80.2° EofN	of Pt. Shoal Lt.	Marshy Rock
J	3188 yds.	78.7° EofS	of Pt. Shoal Lt.	1000 yds. across
J[1]	3855 yds.	66.4° EofS	of Pt. Shoal Lt.	Pt. of Shoals Rk.
K	615 yds.	25.8° EofN	of Pt. Shoal Lt.	4000 yds. across
K[1]	4380 yds.	77.2° EofN	of Pt. Shoal Lt.	Long Shoal and Swash Rock

TABLE II. Summary of depth comparisons at 100-yard intervals over oyster bars in the James River, Virginia. Depths from U. S. Coast and Geodetic Survey hydrographic surveys.

		Means of depths in ft. from readings at comparison pts.			Means of differences at comp. pts. minus 1871-73	1943-48+½*
Trav.	N	1854-55	1871-73	1943-48	1854-55	1854-55 minus
AA[1]	11	5.0	5.7	6.0	—0.59	—0.41
BB[1]	9	0.7	3.6	5.5	—3.00	—4.39
CC[1]	17	7.7	7.2	7.9	+0.46	+0.29
DD[1]	8	4.6	3.9	6.6	+0.75	—1.44
EE[1]	9	9.6	9.6	10.7	0.00	—0.61
FF[1]	18	5.6	7.9	8.5	—2.25	—2.54
GG[1]	36	6.1	6.4	7.6	—0.31	—1.02
HH[1]	19	9.8	9.6	10.4	+0.29	0.00
II[1]	11	9.8	10.5	10.8	—0.73	—0.48
JJ[1]	9	4.7	5.6	6.8	—0.94	—1.72
KK[1]	26	5.0	4.0	6.1	+1.03	—0.62

* Added to offset differences resulting from a half-foot rise in sea level.

News and Notes

AGRICULTURAL SCIENCE SECTION

Dr. K. W. King and Dr. R. W. Engel of the Virginia Agricultural Experiment Station attended the meetings of the Federated Society of Experimental Biologists held at Atlantic City during the week of April 11-15. A paper, entitled "Relation of Diet to Toxicity of Chlorinated Naphthalene in Rats" by Engel, Linkous, and Bell, was presented before the American Institute of Nutrition scientific sessions by Dr. Engel. At the annual business meeting Dr. Engel was elected Secretary of the American Institute of Nutrition for a three-year term.

A new course will be offered for the first time in the fall quarter by the Department of Dairy Husbandry in Public Relations in Dairying. The course deals with local, state, and national dairy organizations; duties of representatives for dairy and service organizations, and the relationship to other groups and individuals, as well as a discussion on promotional, supervisory, and educational problems. It is a senior course and will be taught by Professor P. M. Reaves.

The Department of Dairy Husbandry will be well represented on the program of the American Dairy Science Association's annual meeting to be held at Pennsylvania State University on June 21-24. Three members, Dr. G. C. Graf, Dr. W. A. Hardison, and Professor N. R. Thompson, will present papers. Professor R. G. Connelly and Dr. K. A. Huston will appear on a panel discussion. The Department will also have an exhibit at the meetings.

Mr. Thomas G. Brown of Halifax County has recently accepted the position of assistant soil technologist at the Virginia Truck Experiment Station at Norfolk. Mr. Brown received his B.S. degree in Agronomy at the University of Tennessee in 1950, after having served three years in the Naval Air Corps during World War II. Mr. Rhody B. Hall, former assistant soil technologist, is now an agronomist with the American Agricultural Chemical Company.

Dr. Glenn H. Robinson, a member of the Correlation Staff of the Soil Survey Division of the Soil Conservation Service, U. S. D. A., was assigned to Blacksburg, Virginia as headquarters on April 1, 1954.

Dr. Robinson will be responsible for the correlation of soils mapped in the cooperative Experiment Station and U. S. D. A. Survey in Virginia, North Carolina, and South Carolina. He received his Bachelor's degree from Purdue University, the Ph.D. degree from the University of Wisconsin, and has had a very wide experience in soil classification work both in the United States and abroad.

The first Virginia Polytechnic Institute Agricultural Exposition was held at Blacksburg on May 14 and 15. This was a new endeavor which was sponsored by the various curricula clubs on the campus.

Sidney D. Rogers, Winchester, took top honors in the Little International

and E. A. Drinkwater, Bayard, top honors in the Dairy Club show to feature the 1954 Agricultural Exposition May 14-15.

Don Paarlberg, assistant to the U. S. Secretary of Agriculture, was convocation speaker May 14, and he discussed the Eisenhower farm program, describing it as a compromise between the extremes of government control and full market freedom. Edward A. Wayne, First Vice-President of the Federal Reserve Bank of Richmond, spoke at the Exposition banquet May 15.

Mr. Charles B. Wood has been appointed Research Instructor of Fruit and Vegetable Processing in the Department of Horticulture at Virginia Polytechnic Institute. Mr. Wood is a native of Virginia who received his B.S. degree from Virginia Polytechnic Institute in June, 1954.

Mr. George Goddard has been appointed Research Instructor of Horticulture at Virginia Polytechnic Institute. He will assist in the research and college work conducted at the greenhouses. Mr. Goddard received his B.S. degree from the University of Massachusetts in June, 1954.

Mr. Donald B. Dunlap has been appointed Research Instructor of Horticulture at Virginia Polytechnic Institue. He will assist in the fruit breeding research program. Mr. Dunlap received his B.S. degree from Clemson Agricultural College in June, 1954.—WESLEY P. JUDKINS.

ENGINEERING SECTION

Professor Dan Pletta of Virginia Polytechnic Institute has been asked to serve as a recorder for a discussion group at the National Conference on Higher Education in Chicago. On March 8-10 he attended the Allerton Conference on Solid State Science, sponsored by the National Science Foundation in conjunction with the University of Illinois and Carnegie Institute of Technology.

Members of the Engineering Section attending the annual meeting of the Virginia Society of Professional Engineers at Virginia Beach May 21 and 22 included Professors R. W. Truitt and Dan Pletta of Virginia Polytechnic Institute.

Professors R. W. Truitt and F. W. Martin of Virginia Polytechnic Institute have published a paper in the Journal of Aeronautical Sciences entitled "Effect of After-body Configuration on the Pressure Distribution on Wedges."

Professor N. F. Murphy escorted a number of graduate and senior chemical engineering students from Virginia Polytechnic Institute to the Corrosion Testing Station of the International Nickel Company at Wrightsville Beach, North Carolina on April 26 and 27. Professor Murphy also attended the annual meeting of the Electrochemical Society in Chicago, May 3 and 4.

Professor R. M. Hubbard escorted a group of chemical engineering students from the University of Virginia to the annual meeting of the Mid-Atlantic Regional Group of Student Chapters of the American Institute of Chemical Engineers at Morgantown, West Virginia April 9 to 11, and then accompanied the students on a visit to the Monsanto Chemical Com-

pany plant at Nitro and the Carbide and Carbon Chemical Company Research Laboratory at South Charleston, West Virginia.—ROBERT M. HUBBARD.

SECTION OF GEOLOGY

Dr. Wayne E. Moore is experimenting with the culture of live Foraminifera in the paleontological laboratory at Virginia Polytechnic Institute. He has maintained a live culture of miliolid Foraminifera for more than three months, and has studied the feeding habits, methods and rates of locomotion, and salinity tolerance of these one-called animals. The results of these observations will be useful in ecological studies of the Foraminifera.

The new sedimentation laboratory of the Geology Department at Virginia Polytechnic Institute is nearing completion. The major item of new equipment for the laboratory is a stream table for the study of stream and coastal erosion and sedimentation phenomena. The new stream table consists of a 12-foot trough, which can be tilted and which empties into a 6-foot long tank of standing water. The trough and tank are five feet wide and 18 inches deep. The tank is fitted with glass sides so that depositional structures formed in standing water may be observed. The level of the water in the tank can be changed by 2-inch intervals. The laboratory wil be available for research and instructional use by the fall quarter of this year.

John A. Wood, Jr. received this year's Holden Prize. The prize, a Brunton compass, is awarded annually to the outstanding senior in the Geology Department at Virginia Polytechnic Institute.

The Virginia Department of Highways has published a 70-page bulletin giving the results of physical tests made in connection with their state-wide aggregate survey. More than 2,200 samples were collected and tested in the six-year period of the survey.

Mr. A. B. Cornthwaite, testing engineer, Mr. James Eades, research engineer, and Mr. W. T. Parrott, highway geologist, represented the Virginia Department of Highways at the Fifth Annual Meeting of the "Symposium on Geology as Applied to Highway Engineering" held at Columbus, Ohio. Approximately 150 geologists and engineers from a dozen states attended the meetings.

Dr. Joseph T. Singewald, Jr., professor of economic geology at Johns Hopkins University and director of the Maryland Department of Geology, Mines, and Water Resources, discussed the "Geology and Mineral Resources of Argentina" at the symposium of the Holden Society in connection with the annual Engineering Emphasis Week Program at Virginia Polytechnic Institute.

The Geology Department at Virginia Polytechnic Institute is inaugurating a state-wide study of Virginia building stones. Specimens from all producing areas and other selected localities will be obtained, subjected to laboratory studies, and set into an L-shaped stone wall for long-range observations of their individual weathering and durability characteristics.

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Sandstone and flagstones of possible use for building purposes in the vicinity of the campus will be studied first. Stone for Carol M. Newman Library, now under construction, was selected with the advice and assistance of the geology staff, with the objective of avoiding the somber hue characterizing so many of Virginia's native stone building. The stone being used in construction of the Library is of three types: a bluish-black limestone; a white to light-gray dolomite; and a gray dolomite. Each type of stone weathers a different color.

The Geology Department working under the Virginia Engineering Experiment Station, located at Virginia Polytechnic Institute, is undertaking the following new studies: *Mineralogy of Mine Roof Rocks*——a study of the clay and iron-bearing minerals contributing to the strength and structural integrity of roof rocks in Virginia coal mines; principal investigator, Mr. Carl T. Meyertons. *Virginia Dolomites* —— field and petrographic study of typical Appalachian dolomite-calcite carbonate rocks wih the objective of working out the origin of the rocks; principal investigator, Mr. Charles R. B. Hobbs, Jr. *Petrography and Mineralogy of Virginia Coals*: field and petrographic studies of selected coal beds from the Appalachian Coal Measures with the objective of determining whether these coals can be separated into mineral fractions of special use for industrial purposes; principal investigator, Mr. J. J. Crabb. Mr. Crabb joints the geology staff September 1, 1954, as assistant mineral technologist and assistant professor of geology. *Feldspar-bearing Pegmatites of the Bedford District*——field and laboratory study of the pegmatite-bearing body of crystalline rocks in the areas covered by the Goode and Peaks of Otter quadrangles in Virginia; principal investigators, Mr. William E. Diggs and Mr. George M. Deaton.

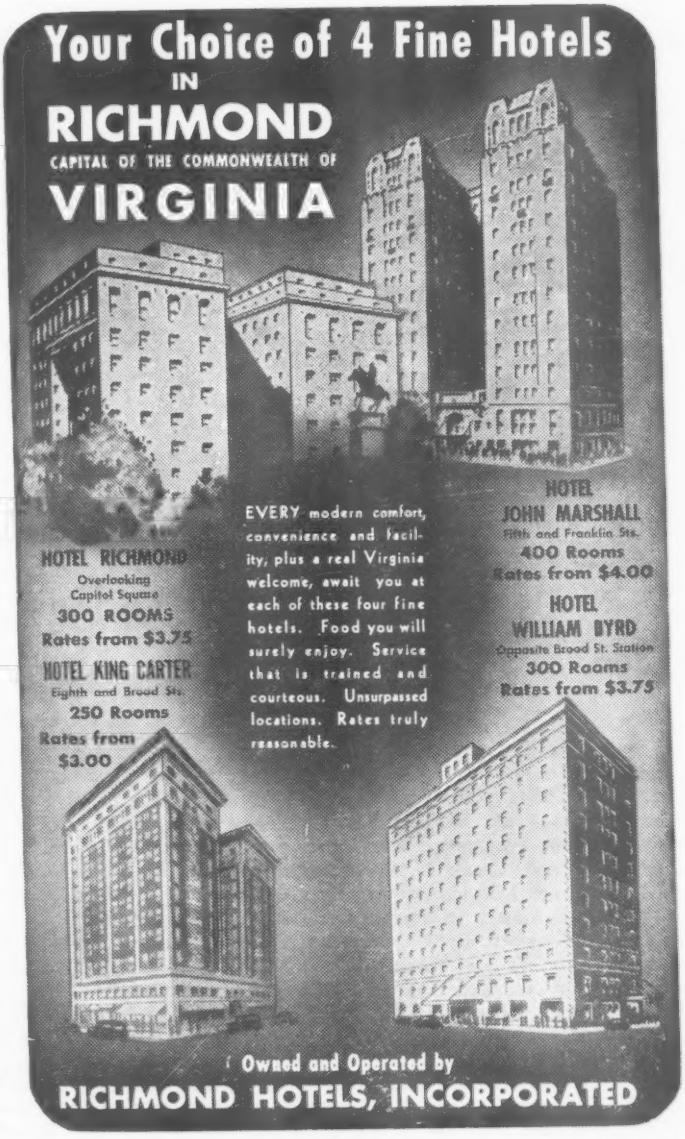
A geochemical laboratory is being set-up by the Department of Geology, Virginia Polytechnic Institute. Vegetation, soil, and water analyses will be made in conjunction with the department's investigations of Virginia mineral resources.

"Geology of the Pilot Mountain Area, Virginia" by R. V. Dietrich was recently published as Bulletin 91 of the Virginia Engineering Experiment Station. The area covered by this report is approximately 175 square miles in Southern Montgomery County.——W. D. LOWRY.

PSYCHOLOGICAL SECTION

The Virginia Examining Board for Clinical Psychologists has recently certified the following psychologists: (1) by reciprocity, Harold N. Hildreth and Charles A. Ullman, both of Arlington; (2) by examination, Samuel S. Dublin, Robert J. Filer, Frederick S. Hauser, Cyril R. Mill, David H. Orr, and Ewing L. Phillips. William M. Hinton was reelected chairman of the Examining Board. Serving with Mr. Hinton on the Board at the present time are the following: Mrs. Catherine T. Giblette, Austin E. Grigg, Richard H. Henneman, and Dr. Gilbert J. Rich.

At its regular meeting in May, the Richmond Psychological Association elected the following officers for 1954-55: President, Dr. Cyril R. Mill,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Richmond Public Schools; Vice-President, Dr. Robert J. Filer, University of Richmond, and Secretary-Treasurer, Dr. Jacob Silverberg, McGuire Veterans Hospital.

Several Virginia psychologists appeared on the program of the 46th annual meeting of the Southern Society for Philosophy and Psychology held in Atlanta, April 15-17. Mr. Frank A. Geldard was chairman of a symposium, *Regional Research and Training Activities in Psychology;* Richard H. Henneman, of the University of Virginia, and Morris Roseman, of the Veterans Administration Hospital in Roanoke, presented papers at the regular sessions. William M. Hinton serves the Society as Treasurer.

At the National Conference on Airborne Electronics held in Dayton, Ohio, on May 10-12, Mr. Henneman read a paper, "A Comparison of the Visual and Auditory Senses as Channels for Data Presentation". This paper included library and laboratory research carried on at the University of Virginia under a research contract with the U. S. Air Force.

Newcomers to state academic circles in the past year were Robert J. Filer at the University of Richmond, and Frederick S. Hauser at Hollins College.

Visiting professors of psychology who will be on the faculty of the Summer School at the University of Virginia are Prof. Henry E. Garrett of Columbia University, distinguished alumnus of the University of Richmond, and former president of the American Psychological Association; Prof. Robert C. Wingfield of Converse College; and Prof. William M. Hinton of Washington and Lee University.

Mr. Frank W. Finger, who spent the academic session of 1953-54 on leave at Yale University, attended the International Congress of Psychology at Montreal, June 7-11.—RICHARD H. HENNEMAN.

STATISTICS SECTION

The Southern Regional Graduate Summer Session in Statistics, sponsored by Virginia Polytechnic Institute, University of Florida, Consolidated University of North Carolina, and the Southern Regional Education Board began July 9, 1954, at Virginia Polytechnic Institute. The faculty for this session includes R. A. Bradley, Virginia Polytechnic Institute; David B. Duncan, Virginia Polytechnic Institute; Ralph E. Comstock, North Carolina State College; Bernie G. Greenberg, University of North Carolina; Boyd Harshbarger, Virginia Polytechnic Institute; Burt C. Horne, Jr., University of North Carolina; Maurice G. Kendall, North Carolina State and University of London, London, England; Roger L. Smith, Virginia Polytechnic Institute; Paul N. Somerville, Virginia Polytechnic Institute; and M. C. Kenneth Tweedie, Virginia Polytechnic Institute who are teaching scheduled classes. There are R. C. Bose, University of North Carolina; W. F. Callander, University of Florida; C. A. Bicking, Department of the Army; James W. Johnston, Jr., Georgetown University; G. L. Edgett, Queen's University, Canada and Virginia Polytechnic Institute; Gertrude Cox, North Carolina State; H. H. Chapman, University of Florida; George F. Gant, Southern Regional Education Board; Besse Day and Francis

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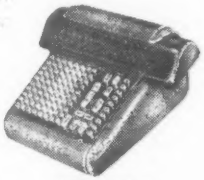

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Del Priore, Naval Engineering Experiment Station; W. A. Hendricks, U. S. Department of Agriculture; and F. J. Anscombe, Princeton University and the University of Cambridge, England who are giving seminars. There are 85 students enrolled. The students come from 24 states and India, Australia, Finland, Canada, Hawaii, the Philippines and China.

Dr. John E. Freund of the Department of Mathematics, Alfred University, New York will join the staff at the Virginia Polytechnic Institute Statistics Department as a visiting professor September 1, 1954. He will replace Dr. Edgett as chief investigator on a contract with the Department of Ordnance. Dr. Freund studied at the University of London, University of California, Columbia University, and University of Pittsburgh. Dr. Freund has published the following: *Modern Elementary Statistics.* New York: Prentice-Hall, 1952; *Elementary College Mathematics.* New York: Prentice-Hall, 1953 (Preliminary Mimeographed Edition); collaborated on the translation from German of Hans Reichenbach's *Philosophy of Space and Time.* (Will be published soon by the University of California Press.) He has also published the following articles: "Segment Functions", "Statistical vs. Pragmatic Inference", "Simplified Computation of the Tetrachoric Correlation Coefficient", "The Degree of Stereotypy", "On the Confirmation of Scientific Theories", "On the Problem of Confirmation", "The Transfer Distribution", "On the Utilization of Direct as well as Collateral Information in Problems of Statistical Estimation", "Some Observations on Laplace's Rule of Succession and Perk's Rule of Indifference", and "The Bivariate Binomial Distribution and Applications".

The following were awarded Master of Science Degrees with a major in statistics at Virginia Polytechnic Institute on June 6, 1954: Robert M. Ableson, William H. Beyer, Edwin Bleicher, Robert G. Bonner, Richard G. Cornell, Patricia A. Ripley, Vincent Schultz, John C. Layman, Paul Sanders. —LIONEL WEISS.